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EARLY EVOLUTION OF HUMAN MEMORY

Great Apes,
Tool-making,
and Cognition

Héctor M. Manrique
Michael J. Walker



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ISBN 978-3-319-64446-2 ISBN 978-3-319-64447-9 (eBook)
DOI 10.1007/978-3-319-64447-9

Library of Congress Control Number: 2017949462

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Printed on acid-free paper

This Palgrave Macmillan imprint is published by Springer Nature
The registered company is Springer International Publishing AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

*In Memoriam to Andrés y Carmen, the most inspiring and loving parents.
And to Matías, the brightest of nephews.*

H.M. Manrique

To Dr. Joaquin Fuster, for his pioneering research into haptic memory.
Michael Walker

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before being appointed in 1988 to establish Physical Anthropology at the University of Murcia. He is the author of *Palaeolithic Pioneers* (Archaeopress, Oxford, 2017) and with Erik Trinkaus of the Washington University of St. Louis has co-edited *The People of Palomas, Neandertals from the Sima de las Palomas del Cabezo Gordo, Southeastern Spain* (Texas A&M University Press, 2017).

ABBREVIATIONS

“Ma”	(= million years ago; Ma is an official scientific abbreviation designated by the International Union of Geological Sciences)
“e.g.”	(= for example, for instance)
“i.e.”	(= that is to say, in other words)
“et al.”	(= and others, and colleagues)
“and refs.”	(= and see bibliographical references contained therein)
“cf.”	(= see also; compare with)
“p.”	(= page)
“pp.”	(= pages)
“etc.”	(= and so on)
“%”	(= per cent)
“ms”	(= millisecond)
“cm”	(= centimeter)

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What This Book Is About

Abstract Experimental findings are reviewed about cognitive inability of great apes, despite intensive training, to use recognition of physical properties of objects to determine how, when, or where to manipulate them as tools for achieving goals. Their cognitive capacity is constrained in situations both of deferred gratification and where available objects were ignored for making a useful composite tool. Apes arguably lack the human cognitive ability to imagine how to blend reality among different potential spheres. This ability requires drawing on memory to envisage alternative future situations, thereby enabling modification of behaviors engrained in procedural memory. Neuroscientific findings are reviewed about short-term working memory, long-term procedural memory, prospective memory and imaginative forward-thinking, with particular reference to manual (“haptic”) behavior. Because wild apes manipulating objects, seeking food, could presage behavioral evolution in early hominins, differences from apes are reviewed. Cognitive implications of stone-tool preparation are considered, drawing attention to aspects of hominin brain evolution and cognitive capacities.

Keywords Behavior • Great ape • Cognition • Memory • Stone • Tool Artifact

This brief critique has two aims. Our first aim is to consider critically (in Chap. 3) just how far great apes show cognitive capacity to bring

and put together inanimate materials in order to assemble tools for their conceivable or preconceived use in particular circumstances. There is a wealth of field observations on the use of objects as tools by great apes in their natural surroundings; the evidence is abundant and undeniable. There is also archeological evidence that in Africa about 3.4 Ma (million years ago) stones were being flaked by australopithecines (bipedal hominoids) who used sharp edges in ways that left cut-marks on animal bones, presumably while scraping meat and fat from bones of dead mammals. If that is correct, then stone tools were made that sometimes were applied to animal remains. Other Primates, in contrast, have not been observed making stone tools for application to animal remains.

The difference raises an important matter of scientific interest which goes beyond merely demonstrating that breaking or even flaking stone can be attributed to both extinct australopithecines and some extant quadrupedal anthropoids, because it raises the question of whether or not only the former (and their human descendants) could hold simultaneously in mind *combinations* or *permutations* of ways to *prepare* stone artifacts with their *possible future uses as tools appropriate for particular purposes*. A significant aspect of making stone artifacts is that one hand has to wield a stone to knap another held in another hand (or foot), and one or both stones must be rotated by hand if flakes are to be removed; some monkeys seem capable of doing that in their natural surroundings, whereas great apes do not appear to do that in the wild. Nevertheless, stones modified by those monkeys do not seem to be applied regularly as tools in attempts to resolve particular tasks in the wild. By contrast, some great apes in the wild have been observed to modify objects in order to achieve particular goals, though these objects are mostly of organic material (such as twigs, stalks, and leaves) rather than inorganic; furthermore, even when they are mineral, typically one stone is not held within one hand (or foot) for modification or flaking by being struck by the "hammer"-stone wielded by another.

Rarely are field observations recorded under such rigorously controlled conditions as might allay the concern of an alert reader about the extent to which a wild Primate shows not only foresight about how a simple tool can be used, but also its cognitive ability to have combined such foresight with insights regarding appropriate or inappropriate choices by it of particular physical attributes required to use the tool in order to solve a task correctly, particularly, when changes are imposed either on the intrinsic materials available for making tools or on the extrinsic conditions for their use.

Often researchers who have considered the matter have interpreted empirical observations in the wild on nonhuman Primates in terms of inferences about human evolution by weaving together primatology, anthropology, and psychology. Although several inferences are indeed plausible conjectures, the arguments are accommodative in so far as they are irrefutable from an epistemological standpoint. In short, there is a methodological deficit. They lead to a self-serving approach that lacks the critical skepticism of careful experimental scientific inquiry which aims to test an uncertain working hypothesis that there should follow a particular detectable consequence that is predicted if, *and only if*, such-and-such phenomena are also present. Therefore, inferences derived from empirical observations on tool-making and tool-use by apes in the wild need to be contrasted against the outcomes of rigorously controlled experiments on apes in the laboratory.

Well-defined experimental conditions are fundamental when investigating a specific variable, in order to control for or neutralize, possibly incidental variables or extraneous aspects that otherwise may impinge on experimental outcomes and thereby reduce scientific confidence in them. Controlled conditions are essential in order to refine and define the theoretical constructs under investigation, the extensive foundations of which here lie in Human Psychology. Methodological matters of scientific research design must be subjected to rigorous critical scrutiny. In relation to any particular problem to be solved by an animal, account must be taken of any previous experience it may have acquired in broadly commensurate tasks. This may lead a critical student to reflect on whether those could have provided it with some understanding of the causal requirements for solving the problem (for instance, topological or mechanical concepts), or on the contrary, whether after repeated trial-and-error its understanding was no more than superficial: the dilemma may preclude firm conclusions from being drawn about its cognitive capabilities.

Trial-and-error undoubtedly plays a part in human learning. Indeed, when we face a problem our early attempts toward finding a solution may well involve fairly random thrusts, whether mental or manual, that can give us insights into underlying principles about relationships between things. Perhaps, the best demonstration of deep, causal understanding of a problem is shown by a capacity to solve other problems when we discover that they all share a causal structure in common so that we come to recognize that what appear to be differences between them are contingent aspects and not *really* fundamental. This influences

our grasp on reality even when, paradoxically, the grasp is an intangible principle and, moreover, often barely enters our conscious awareness. Far from being a “eureka moment” of heightened awareness and marvelous inspiration, the grasp is usually a humdrum “matter-of-fact” intuition about how to perform a task better, meeting our requirements satisfactorily without arousing our curiosity much. In Comparative Psychology, the study of cognition in nonverbal anthropoid Primates (including preverbal children) and, in particular, the investigation of mental “transference” between remembered experiences of different outcomes of various tasks undertaken by a subject that share an underlying causal structure, have been the object of disparate methodological approaches, including some, especially concerning episodic memory, that are of questionable validity whenever they involve modification of theoretical constructs and concepts borrowed from Human Psychology. Therefore, in Chap. 3, critical consideration of methodological matters is given to studies undertaken on animals either in captivity or with such controls on their freedom as to offer a guarantee of reasonable experimental control.

One of us, Héctor Manrique, teaches Developmental Psychology at the University of Saragossa (Zaragoza) in Spain; he spent two-and-a-half years studying great apes at the Leipzig Max Planck Institute for Evolutionary Anthropology in Germany. Consideration of experiments conducted there, as well as some published at other research centers, has led him to argue that challenges can be made, usually on methodological grounds, to some claims that great apes can show cognitive capacity for conceiving of the bringing and putting together of inert materials in variable ways that demonstrate consistent behavior for solving various and varying tasks variably. In short, generally speaking, they show little ability to imagine possibilities that might be conjured up, such as novel tools-to-be, in order to extend or expand behavioral routines. Such conceptual limitations may not be unrelated, Héctor Manrique suggests, to constraints on the development of a “theory of mind”. Put in another way, in visual perspective-taking, just as in belief-attribution, it is necessary to keep in mind different, sometimes even contradictory, representations of reality; for instance, a mental representation of a likely tool, as yet inexistent but soon to be made, at the same time as a representation of the raw material visibly held in hand. Whilst great apes are extremely inventive and able to solve new problems that require use of tools, serious doubts are raised as to whether they can represent and compare, mentally, different aspects of reality in order to combine them in new

and sophisticated ways, particularly when required to imagine things that they themselves have not experienced before: discussion of this matter is obligatory for comparing tool-making in great apes with human tool-making. This is not to declare that great apes in their natural surroundings lack complex cognitive capacities. Moreover, a possibility cannot be discounted that difficulties with experimental design may have led to some contradictory results, thereby confounding confusion.

The matter, nonetheless, needs to be complemented by considerations of other matters outside the scope of experimentation but which are grounded on undoubted material or scientific findings. They include, on the one hand, the undeniably hard evidence of stone tools in a Paleolithic record that in Africa extends as far back as 3.4 Ma (million years ago). On the other hand, they also include neuroscientific findings about cerebral neuronal activity related to manipulation of tools in anthropoid Primates, both human and nonhuman; in that regard, findings concerning Human Psychology lack sufficient scientific rigor to warrant more than passing comment, with a few exceptions. Therefore, we eschew referring to publications that do not deal directly with comparative experiments in higher Primates, the Paleolithic record of stone tools, or neuroscientific investigations about manipulation of objects.

Thus, in part, our critique arose from disquiet by Héctor Manrique about claims for a noteworthy capacity of great apes to create tools purposefully beforehand, for the fulfillment of a need, solution of a specific problem, or achievement of a particular task, because critical methodological scrutiny of the design of much laboratory experimentation purporting to substantiate such claims hardly inspires overwhelming confidence in them.

In part, furthermore, our critique, and our second aim, arose from disquiet by the other of us, Michael Walker, over widely held preconceptions which are: first, that the process of the evolution of cognitive capacity in Hominini encompassed both a *late* component, namely, the appearance, during the past quarter-of-a-million years, of putative “modern” behavior (often ascribed uniquely to *Homo sapiens*), and, from long *before* that time, an “archaic” component of hominin behavior (which may have persisted afterwards, for instance in Neandertals); and second, that, in some hard-to-explain manner, the component arose of “archaic” behavior, which included using one stone to strike and flake another stone so as to create a cutting edge for use as a tool that left cut-marks on bones, thereby allegedly conferring an adaptive selective advantage

over other hominoid paleospecies in which that behavior had not arisen, and for which, were it ever to have appeared in one or another, it is presumed (post hoc ergo propter hoc) to have conferred none, disappearing almost without trace in the paleontological hominoid record. Neither manual anatomy nor cerebral neuronal circuitry need have prevented them from flaking of stones which, indeed, is practised by some wild monkeys today though their products are hardly if ever used as tools, let alone wielded to leave cut-marks on bones. In contrast, “archaic” hominin behavior included preparation of stone tools used sometimes to cut animal carcasses, requiring a chain of differentiated activities carried out sequentially with foresight. Evolutionary achievement of such foresight implies a gradual process (maybe originating as an exaptation of aimless stone-flaking) favoring reproductive success by natural selection which led to enhancement of cerebral neuronal circuits that enabled imitative learning by observation. Natural selection implies imperceptible evolution and a mind-numbingly slow process of genetic incidence on neuronal activity.

We argue that neurobiological considerations of the evolution of the hominin brain, based on neuroscientific research, render likely a plausible working hypothesis of a significant change in tool-making and tool-use involving stone during the Late Pliocene. We argue, moreover, that further significant change took place during the Early Pleistocene in the genus *Homo* which underpinned later human behavior. We propose that this change involved evolutionary developments in cerebral neuronal relationships particularly between short-term active haptic attention (short-term working memory for tactile behavior) and both long-term, implicit, procedural memory and also prospective (future) memory that enabled insights about the usefulness and feasibility of novel conjunctions of separate objects by putting them together and the envisaging therefrom of alternative imaginary topological possibilities, which, it is conjectured, might have fostered an emergent “theory of mind”, thereby sowing the seeds of “modern” behavior. In contrast to some studies of the evolution of memory, we regard haptic attention and the evolution of implicit procedural memory in hominins as having been as relevant as visual input and the evolution of explicit episodic memory. Our proposal has both methodological and epistemological implications for human cognitive evolution.

We have begun, above, to touch on our second aim. It is the object of Chap. 4 which contains two complementary albeit different lines

of argument. They arose by serendipity involving Michael Walker, Honorary Emeritus Professor in the Department of Zoology and Physical Anthropology at the University of Murcia in Spain. Presence of early *Homo* from 1.2 Ma is well documented in Spain. Excavation by Michael Walker's research team of a singular 800,000-year-old Paleolithic assemblage from about 0.8 Ma at Cueva Negra del Estrecho del Río Quípar, in Murcia, containing both an "Acheulian" bifacially flaked hand-axe and cores and flakes made by hierarchical ("Levallois") repetitive flaking of prepared cores (as well as remains of fire), overturned received wisdom that had attributed the appearance of both kinds of stone tools in Europe to a later time (about half-a-million years ago). It also posed intriguing paleoanthropological questions about *how* people at such an early time might have kept in mind such different very ways of making stone tools, and about *how* memory might have been implicated.

Mental agility is attributed to *Homo sapiens* alone by many anthropologists who opine that before the species arose (about 300,000 years ago in Africa) the behavior of archaic forms of the genus *Homo* was unimaginative and stereotyped. They include both *Homo neanderthalensis* and its precursor *Homo heidelbergensis* (both occur in Spain, as elsewhere in Europe), as well as even more ancient forms such as *Homo erectus* that is found in Eurasia quite soon after having arisen in Africa (where an early form dating from almost 2 Ma is called often *Homo ergaster*). Whereas excavated stones were flaked (and used, as cut-marks on bone imply) by australopithecines in Africa as early as 3.4 Ma, it is most likely that African early *Homo* was responsible for both the earliest known bifacially flaked hand-axes (about 1.8 Ma) and the earliest known hierarchical repetitive flaking of prepared cores (about 1.3 Ma). Even before 1 million years ago, those flaking techniques are documented at some sites outside Africa, though to date the earliest of these where both techniques are found *together* is Cueva Negra del Estrecho del Río Quípar. This demonstrates that stone-knappers there possessed *both* manual dexterity and *cognitive versatility*.

That bifacially flaked ("Acheulian") hand-axes imply a cognitive appreciation of topological 3-dimensional *symmetry* was proposed in 1989 by archeologist Tom Wynn. Moreover, he argued that an idea of "*the whole tool*" would have had to have been "*conceived ahead of time*" "*in the mind of the knapper*" (Wynn 1989, p. 63) There is no overwhelming evidence that great apes show this cognitive capacity, whether from observations in the wild or the laboratory. Furthermore, an

appreciation of 3-dimensional *asymmetry* is required for extracting flakes by hierarchical repetitive knapping of prepared (“Levallois”) cores. In short, stone artifacts made about a million years ago permit two important inferences to be drawn: first, that great apes lack the cognitive abilities possessed by some forms of archaic *Homo* that, second, behaved in ways that are recognizably *human*. These indeed were different from those that can be inferred from archeological assemblages left by skeletally speaking “modern” *Homo sapiens* during the last 100,000 years. In that regard, however, in Chap. 4, disagreement is expressed, concerning the part played by the evolution of *memory*, with views made popular by Tom Wynn and psychologist Fred Coolidge (Coolidge and Wynn 2005, 2007, 2009; Wynn and Coolidge 2012). Whereas, they have given pride of place to neuropsychological considerations of (short-term) working memory, Chap. 4 argues for a greater role for the evolution of (long-term) procedural memory (see below).

The serendipity was that co-author Michael Walker is not only an anthropologist (who had studied under hand-axe expert Derek Roe who was Professor of Palaeolithic Archaeology at Oxford University), but also a medical graduate and physiologist who in his younger days had developed a long-standing interest in neurophysiology which underlay a lingering doubt that evolution of cognition in *Homo* was always and everywhere consequent on evolution of its skulls and their erstwhile brains. Whereas Coolidge and Wynn infer from neuropsychological considerations about modern humans that Late Pleistocene skilfulness in tool-making reflects the evolution of working memory, Chap. 4, in marked contrast, develops what is considered to be a more plausible argument, grounded in empirical neurophysiological and neuroscientific evidence about tactile or “haptic” working memory (demonstrated in the brain cells of live monkeys by UCLA’s Joaquín Fuster: Fuster 1999). It is proposed that natural selection on genetic and epigenetic tendencies impinged on neurons in early *Homo* brains and gradually favored bio-physical circumstances for the eventual enhancement of neuronal propensities for long-term (nondeclarative) procedural memory and the development of cognitive versatility appropriate for envisaging how manual dexterity might be applied differently in order to knap a variety of stone tools. It is suggested that the notion proposed twenty years ago by some psychologists of “long-term working memory” may not be quite the contradiction in terms that it seems to imply at first sight, and that it might even help towards interpreting some stone-knapping behaviors of

australopithecines and early *Homo*, though it is unclear how it might be represented in terms of cerebral neuronal circuitry.

It is argued in Chap. 4 that observational learning most likely was enhanced by mirror-neuron circuits in parietal and prefrontal cortical regions of archaic human brains, and that they modulated hippocampal neuronal responses in the medial temporal cortex which play a part in transmission of forward thinking (prospective memory) to frontal and other parts of the brain. (Very likely selective tendencies enabled a wide variety of tools to be made from perishable materials: from 400,000 years ago, in the Middle Pleistocene, finds of long wooden spears point to the cognitive capability and technical skills that archaic *Homo* needed to fashion them, though the lack of Pliocene and Early Pleistocene artifacts made from perishable materials renders those spears fundamentally incommensurable with perishable objects modified or used as tools by great apes today, and therefore, in order to compare like with like, we are constrained to considering artifacts that are commensurable, by having been made from imperishable materials, as being those most appropriate for interspecific behavioral comparison or contrast.) More to the point, neuroscientific data that implicate neuronal activity in the anterior supra-marginal gyrus of the left inferior parietal lobule when tools are used by modern humans suggest a specific evolutionary development in our lineage vis-à-vis other extant anthropoid species. Considerations are offered about how the evolution of archaic human brains is likely to have been related to the particular pattern of evolution of archaic human developmental anatomy before biological maturity was attained by individuals, which seems to have been different from that of great apes on the one hand, and modern humans on the other.

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Tool-Use by Great Apes in the Wild

Abstract Evidence for tool use and tool-making by great apes in the wild is contrasted against the earliest stone artifacts and signs of their use before 2 million years ago by hominins who had attained a cognitive capacity both to envisage how by manipulating one object they could modify another in order to transform it into a tool, and to remember the manual behavior required to carry out the procedure.

Keywords Behavior · Chimpanzee · Cognition · Hammer · Hominin Memory · Stone · Tool

Among several claims for their ingenuity with tools are observations of chimpanzees using sticks, twigs, stalks, leaf midribs, or petioles, in order to feed on termites, either “fished” out from ant hills that first have been perforated with rigid sticks, or lifted up on plant materials dipped into ant trails (Goodall 1986; McGrew 1974, 1992; McGrew and Tutin 1978; McGrew et al. 1979; Sabater 1984a; Van Lawick-Goodall 1970). Other observations range from using leaves as sponges to draw water from holes in tree trunks (Goodall 1964a), using sticks to extract honey from hives of wild bees (Brewer and McGrew 1990; Boesch et al. 2009; Izawa and Itani 1966; Stanford et al. 2000), to beat fruit-bearing trees (Sabater 1974a, b, 1984a, b, 1992, 1993), to fend off leopards (Boesch 2009; Jones and Sabater 1969, 1971; Kortlandt 1965),

to throw (Goodall 1964b), or to hurl in attempts to bring down prosimians (Pruetz and Bertolani 2007), not to mention using stones for cracking open kernels or stones in fruit (Beatty 1951; Matsuzawa 1991; Rahm 1971; Struhsacker and Hunkeler 1971; Sugiyama and Koman 1979). Perforation of ant hills with rigid sticks, followed by the introduction of pliable stalks with chewed brush-like tips to maximize ant collection, may reflect a capacity to devise a complex tool kit (Sanz et al. 2004; Sanz and Morgan 2007). During different stages of extraction of honey from hives, manipulation has been observed of up to five sticks differing in rigidity (Brewer and McGrew 1990; Stanford et al. 2000). Such tool kits seem to show that chimpanzees both recognize appropriate properties of things to be chosen for a given task and can plan the order of their deployment.

Cracking kernels open may involve chimpanzee tool kits comprising an “anvil” (such as a rock or a tree root), on a relatively flat surface of which a kernel is set that is broken open using stone or wooden hammers (Humle and Matsuzawa 2001; Matsuzawa 1991; McGrew 1992); chimpanzees may seek out and then carry appropriate stones for use as both hammers and anvils to where they will be used, perhaps aware that both are needed to crack kernels (Carvalho et al. 2013). Analysis of the artifacts employed as anvil or hammer in an outdoor laboratory at Bossou revealed that chimpanzees tend to prefer wider and lighter objects to be used as hammers, while height or length do not significantly differ, which reinforces the notion that both anvil and hammer might be perceived as an integrated working unit (Carvalho et al. 2008). Sometimes a third stone is wedged below the anvil to keep its surface horizontal (Humle and Matsuzawa 2001; Matsuzawa 1991; McGrew 1992). It has been argued that such behavior may have arisen quite late during the Pleistocene (Haslam 2014). Wild panins more often use plant-derived tools. Gorillas in the wild have been reported to use sticks to reach fruit on a tree (Pitman 1931, cited in Sabater 1984b) and to gauge the depth of water when wading (Breuer et al. 2005). In addition to the hominoid taxa mentioned above, some of those activities, especially manipulation of stone, are reported in other anthropoid Primates, both in catarrhine (Malaivijtnond et al. 2007; Gumert et al. 2009; Haslam et al. 2013) and platyrrhine monkeys (Cummins-Sebree and Fragaszy 2006 and references therein; Visalberghi and Fragaszy 2013 and references therein; Proffitt et al. 2016); although the anatomy of their hands is clearly compatible with such behavior, their cognitive

understanding of it is far from clear, nor do they regularly use as tools the stone products of their manipulations. Plausibly, some stone artifacts uncovered by archeologists could owe to nonhuman anthropoid behavior (Fiedel 2017; Haslam et al. 2009).

Raw stones from Olduvai Gorge in Tanzania were used to crack nuts by chimpanzees at the Japanese Kumamoto Sanctuary of the Kyoto University Wildlife Research Center, and, after use, detailed inspection of stones, including microscopy, enabled interesting comparisons and contrasts to be drawn, both with stones used in like fashion by humans and with Paleolithic finds excavated at Olduvai which show more modification of working surfaces than those used by the chimpanzees (Arroyo et al. 2016). The findings chime with those from a comparative analysis of stone cores, flakes, and fragments from the 2.6 Ma site of Gona in Ethiopia (commonly attributed to *Australopithecus garhi*) were compared and contrasted with those produced by humans and by captive bonobos that had learnt how to knap a stone core held in one hand by wielding a hammer-stone held in the other; the bonobos did not attain the degree of core-reduction or the frequency of parallel-sided flakes observed in the Gona assemblage, and produced more edge-battered cores and broken flakes and fragments, although the Gona assemblage itself showed a lower degree of core-reduction than that of human knappers (Toth et al. 2006); the research did not extend to use of the modified stones (despite referring to the study, only the ability of the captive bonobos to learn percussive technology from one another has captured the attention of Whiten 2015). Excavation at the 2.34 Ma Lokalelei site in Kenya has allowed reconstruction of the knapping sequences of cores, by refitting flakes and fragments, which testifies to the accuracy with which hominins knapped stone and implies their ability to strike cores repeatedly on angular surfaces recognized as propitious for removal of flakes (Delagnes and Roche 2005; Roche 2005). For efficient (“conchoidal”) flaking of siliceous rock, an appropriate surface angle is one that does not exceed 90°. Trained bonobos seem to find it harder than human apprentices to remember to take advantage of this. A recent analysis concluded that “transition from anvil and hammer percussive techniques (such as nut-cracking) to freehand knapping techniques in early hominins necessitated improved perceptual abilities, learning capacities, and bimanual dexterity superior to that of non-human Primates” (Bril et al. 2015).

It should be borne in mind, however, that nonhuman wild Primates do not modify a stone in order to use it for modifying another object

Table 2.1 A convenient classification of both present-day Hominoids and some extinct Pliocene and Pleistocene genera

<u>A convenient classification of both present-day Hominoids and some extinct Pliocene and Pleistocene genera</u> (alternative classifications exist)				
superfamily	H o m i n o i d e a			
families	H o m i n i d a e		P o n g i d a e	H y l o b a t i d a e
subfamilies	H o m i n i n i	P a n i n i	P o n g i n i	H y l o b a t i d i n i
genera (or subgenera)	† <i>Ardipithecus</i> † <i>Australopithecus</i> († <i>Paranthropus</i>) <i>Homo</i>	<i>Gorilla</i> <i>Pan</i> gorillas, chimpanzees, bonobos	† <i>Gigantopithecus</i> <i>Pongo</i> orangutan	<i>Hylobates</i> (<i>Symphalangus</i>) gibbons, siamangs
† = extinct				
Note: Within the order Primates and its suborder Haplorrhini, the infraorder Simiiformes (anthropoid Primates) is often divided into Platyrrhines (New World monkeys) and Catarrhines (Old World monkeys, which have tails, and Hominoids, which do not). Gorillas, chimpanzees, bonobos, and orangutans are called often "great apes" because of their size.				

that *thus transformed is then used as a tool*. Just when that procedure began to characterize the activities of human forerunners early on is a matter of great interest both in the study of human evolution and for understanding the evolutionary trajectory of human cognition *in relation to memory*; our principal concern is with this particular aspect of the matter. It is for this reason that we give pride of place to the modification of one stone by wielding another in order to make a usable tool. This requires more than the simple awareness that an unmodified or slightly modified object can be handled as a useful tool for attaining foreseeable short-term goals (perhaps for immediate achievement of speedy gratification) with which its evident physical properties are perceived as being sufficiently commensurate. It requires *remembering* how two “unpromising” objects (stones) can be made to react with each other, by being moved differently by the right and left hands, in order that one or more products of such reactions may be suitable for application to tasks that may not be limited to immediately attaining an obviously foreseeable goal, but instead may involve forward planning of activities, based on the *remembered* experiences or different circumstances that could be *envisaged* (and perhaps implying that gratification may be deferred for some time after the tool has been made) (Table 2.1).

The nature of the geological record is such that stones, bones, and teeth are preserved far better than softer materials, including wood, and therefore are the principal raw materials on which commensurable analysis of modification can be carried out for rigorous comparison or contrast

with experimental modification of objects either into artifacts or caused by their use as tools (wooden artifacts have not survived from before 0.5 Ma). Our inquiry into the evolution of human memory therefore is constrained by the nature of the archeological record itself. Assuredly our hominin ancestors made and used tools from a wide variety of perishable materials, but plausible conjectures drawn from primatology or ethnography about what likely they may have made or used from perishable materials are not particularly helpful in considering how human memory probably evolved.

Tool-use in the wild by chimpanzees, and their ability to modify natural substrates in order to improve tool functionality, underlie a conjecture that their behavior can be compared with that of Australopithecines. This may be a risky conjecture, grounded in a superficial reading of alleged tool-related achievements by nonhuman Primates, rather than rigorous analysis of the underlying cognitive complexity of their use and modification of tools. Herein lies the rub. In short, comparing the technology of chimpanzees and early humans is more than just a matter of detailed analysis of the physical features of the objects themselves; it requires taking into account the cognitive capacities implicit in their use or preparation.

Producing apparently comparable technological outcomes need not imply recruitment of *identical* cognitive processes, because *analogous* cognitive capacities can lie behind the production of apparently similar technological outcomes as circumstances require, albeit with different functions. Thus, whereas a washing machine and a refrigerator may present external features in common (a big white box, so as to fit in with kitchen décor), their internal structures and functions differ utterly; contrariwise, a circular washing machine shares more technology in common with a box-like one than with a refrigerator. Such paradoxes exist in very simple tools indeed; thus, a ladle for serving soup looks superficially like the ladle with which Spanish grocers serve customers with olives extracted by it from a tub, with the fundamental difference that this ladle has holes to strain off the liquid that has conserved them.

Late Pliocene Australopithecine stone artifacts will be considered from a standpoint of prerequisites for cognitive capacity and brain circuitry, leading up to consideration of behaviors involving tool use and the resolution of problems demonstrated by recruitment of similar cognitive processes by chimpanzees, be they in the wild or captivity. Ostensive similarity between the apparent structures of tasks will be side-stepped here, in order to pay attention first and foremost to cognitive requirements

that are linked causally. Diverse tasks resolved by *Pan* and *Homo* will be analyzed such that the cognitive capacities underlying them may be considered in a range of problems, with disregard to the external form of each. Where a specific problem can be approached from only one angle, it yet may be possible to infer from the cognitive capacities of another genus that a solution may lie within its grasp (albeit beyond the possibility of experimental demonstration in the laboratory, perhaps owing to lack of sufficient motivation in artificial circumstances).

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Great Apes, Tools, and Cognition

Abstract Careful analysis casts doubt on the appropriateness of the methodology of several experiments claiming to show that apes have a developed cognitive capacity to make and use tools. It is argued that inappropriate experimental design mostly precludes clear-cut conclusions from being drawn.

Keywords Deferred gratification · Working memory · Short-term memory · Haptic manipulation · Long-term memory · Procedural memory · Prospective memory · Planning · Perspective-taking
Theory of mind

3.1 RECOGNITION OF FUNCTIONAL PROPERTIES OF TOOLS

Making stone tools with functional properties suitable for foreseeable tasks requires prior choice of raw material with appropriate physical characteristics. Do great apes have the cognitive capacity required for such choice? Can they recognize and distinguish the relevant physical properties—and neglect irrelevant ones—in relation to a specific problem? They can both assess task requirements and recognize properties or affordances of tools that satisfy those (Manrique et al. 2010; Manrique and Call 2011). In one experiment (Manrique et al. 2010) a banana or a bunch of grapes were hung out of reach of a caged great ape (chimpanzee, bonobo, gorilla and orangutan), and on a platform outside the cage there were

placed three “stick-like tools”, hitherto never seen by the animal, from which it could take only one; of the three, one alone was rigid enough to reach the hanging fruit. The sole information available to the ape came either from its prior haptic manipulation of the objects before the reward was hung, or watching a researcher who during five seconds was engaged in trying to bend and unbend each tool. Nevertheless, individuals belonging to the four great ape species were able to identify the only one rigid enough to reach the fruit, despite never having used it for that purpose. The handler’s mere demonstration sufficed for apes to recognize those properties of the tool appropriate for solving the task. Furthermore, the properties of rigidity were never demonstrated specifically or exclusively, instead the demonstrator simply manipulated the objects in full view of the animals that had to choose from those properties they perceived (smell, color, length, texture, rigidity, etc.), of which rigidity alone enabled the fruit to be reached. The success rate of around 90% of trials far exceeded an anticipated success rate by chance of around 33%. Therefore, great apes seem able to generate a notion of rigidity that cannot be inferred from the appearance of an object but can guide their choice.

Moreover, flexibility of choice exists. If the fruit in the foregoing study was replaced by a reward of fruit juice in a container, the edge of which was at a 90° angle from an animal’s mouth, the apes took from the three objects the only flexible tube, and no longer a rigid one (shown to be useless), indicating that they had paid attention to the requirements of the new task and that this overcame any negative response to the flexible item which might have been induced by their rejection of it in the previous task. In like vein, orangutans that spontaneously had learnt to use a tube as a straw to drink juice from a container were observed to choose and unblock unfamiliar ones that had been blocked in order to turn them into functional tools to drink with. When presented with unfamiliar tubes in a subsequent selection experiment they rapidly identified and picked out those tools that were functional, that is to say hollow and without holes in the sides that would render them useless, thus here again they disregarded irrelevant features of the tools in favor of those relevant to the task (Manrique and Call 2011). The findings support the likelihood that were great apes to seek raw materials for stone-tool production they would be capable of choosing suitable ones. This inference accords with the aforementioned observations on tool-use in the wild, though interpretation of those is limited by the impossibility of knowing whether, say, wild chimpanzees recognize functional

properties needed to execute particular tasks, or whether they come to link tools that give them satisfactory outcomes with particular aspects of those tools, such as color, smell, texture, etc., that could influence their choices without any appreciation of rigidity or other properties that are fundamentally necessary for the tools to be of use in the tasks. This is an ever-present epistemological and methodological difficulty with the interpretation of seemingly intelligent animal behavior, in particular situations in the wild, in the absence of knowledge about precisely how, when, or where it arose. Controlled experimental studies are therefore a necessary complement to field observations.

3.2 DEFERRED GRATIFICATION

When our distant human ancestors were hard at work making tools, before getting any reward from the fruit of their labor they no doubt spent much time and effort that demanded attention which both could have been given to behavior affording readier gratification—such as eating, sexual activity, or simply resting—and which also must have required them to control those impulses that usually cause overriding immediate responses to stimuli from their surroundings. Their ability to divert attention away from such stimuli, and devote themselves to less appealing, time-consuming tasks, reflect a cognitive capacity for self-control that was surely fundamental for technological Paleolithic developments in the Late Pliocene and Early Pleistocene. Some self-control can be seen in chimpanzees in experiments involving deferred gratification where an immediate small reward is rejected in the hope of getting a better reward later on.

The well-known “marshmallow” experiment highlighted deferred gratification by showing that children below school-age could resist temptation in anticipation of an eventually better outcome (Mischel and Ebbsen 1970). Children were offered a choice between receiving either one marshmallow immediately or two if they waited for about fifteen minutes, during which time the tester disconcerted them by leaving the room but then returned. The mental processes were assessed that enable a young child to forego immediate gratification and, instead, to wait for a more desirable albeit deferred reward (Mischel et al. 1989).

A century ago, it was observed that chimpanzees could hold back an impulse to satisfy an immediate need in order to obtain a better reward by using a tool (Köhler 1917, 1921, 1925), which was interpreted as an extension of the process of indirect thinking: thus, if tool-use is

considered to solve a problem, then an immediate desire, such as getting at the kernel of a nut, must be set aside, or inhibited, and replaced by one or several intermediate objectives, such as first finding or producing an appropriate tool.

Latterly, chimpanzees have been the object of versions of the marshmallow experiment (Beran et al. 1999), in which the animals either could wait for a better reward (delivered some minutes later) or press a button to take a reward placed beside it. When the immediate reward was the better one, such as a banana instead of carrot, they pressed immediately, whereas they waited for about three minutes when the poorer reward was beside the button. Subsequent variations included whether the chimpanzees were allowed or not to see how rewards accumulated, whether the researcher was present or not in the room, and extension of the wait to fifteen minutes (Beran and Evans 2006).

Further studies have explored the capacity of chimpanzees to prolong their wait by an intentional behavioral strategy. One study (Beran and Evans 2009) has investigated whether chimpanzees, like children (Peake et al. 2002), employ distractor tasks as a strategy for increasing the efficiency of deferred gratification tasks. In this study, a dispenser was programmed to release up to 36 fruit-flavored candies through a tube into the chimpanzee's cage and to cease releasing them when an animal disconnected the tube in order to eat them. Three alternative experimental situations were compared. In the first, the animal waited passively during release of the treats. In the second, it was allowed to play with a computer with which it was familiar, though this activity did not affect the rate of release of the sweets which was the same as before. In the third situation, the chimpanzee's activity with the computer involved a task that affected release of the candies, thereby enabling the animal to influence release; the computer-play distracted the chimpanzee's attention away from the food whilst affording it a possibility to maximize the quantity that had accumulated before taking some and thereby stopping further release. Of four chimpanzees tested, three showed no differences in the deferred gratification task whichever situation they were in. Only one benefitted from the third situation which afforded the possibility that distracted behavior could increase the rewards, as young children readily discover (Peake et al. 2002) who defer gratification longest when they carry out a concurrent distracting task (whilst performing well whether performing the task is linked to delivery of rewards or not). However, in a variation of the accumulation task chimpanzees did

engage in distractive activities more often when the dispenser that delivered food was inside their cage, and hence accessible, as against to when it was outside and no self-control was needed (Evans and Beran 2007). Perhaps, the divergence in the results owes to the methodological variations of the task and, critically, whether the food rewards were delivered inside or outside the subjects' cage.

Fewer studies have investigated the ability of bonobos (*Pan paniscus*) to defer gratification. One employed an accumulation task (Stevens et al. 2011) in which grape halves were delivered at a maximum rate of one every 5 seconds until ten pieces were amassed. Delivery ceased whenever subjects tried to grab a half-grape. Their capacity to delay gratification seemed more limited than that of chimpanzees because only two accumulated ten grape halves, thereby showing a capacity to wait for almost a minute. However, performance worsened with unreliable or unpredictable provision, with one in four subjects behaving more impulsively when reliability of grape-delivery was manipulated by the experimenter.

Experiments that incorporate distraction tasks seem a better way to identifying the deferred gratification and self-control that are recruited when making stone tools than are "Go/NoGo" tasks. In the latter, inhibitory capability is fundamental to success, as demonstrated in experiments in which chimpanzees had to indicate which was the lesser of two quantities of rewards in order to be given the larger one (Boysen and Berntson 1995) or had to refrain from reaching directly for a reward and instead had to reach indirectly to grab the reward from behind (Vlamings et al. 2010). In both of those cases, self-control need not be the only possible explanation for their successful achievements because these could be merely outcomes of inhibition were the animals to have found by associative learning that overcoming a prepotent response led to a better reward. In contrast, experiments that incorporate concurrent tasks are more appropriate for analogical comparison to the process of making a stone tool, because the stone knapper must exercise restraint from engaging in behavior affording immediate satisfaction (for instance, feeding on nearby berries, low in caloric value) in order to undertake tasks conducive to gaining long-term advantages (for instance, scraping fat, of high caloric value, from an animal lying dead three kilometers away), notwithstanding noteworthy expenditure of energy in carrying out a complex chain of activities which requires premeditation and conscious contemplation of substantial delay before worthwhile recompense can be achieved.

Early in human evolution, might tool-making have played a part analogous to the distraction effect afforded by the computer? A long delay, likely to have been at least an hour, would have elapsed between starting out to create a tool and gaining an enjoyable reward by manipulating it. This implies noteworthy evolution in human ancestors of capacities for different kinds of memory and their interplay in configuring Paleolithic behavior: especially haptic working attention (short-term memory), haptic procedural memory (long-term and perhaps short-term), and prospective memory. Neurophysiological aspects of that evolution must be considered in some detail. Furthermore, it probably implies also a capacity for envisaging and maintaining representations that are distinct from representation of that reality which *is*, and against which they are juxtaposed as what *could* be or what *will* be. This implication is not unrelated to aspects of “perspective taking” and “false belief” that are relevant for the development of a “theory of mind” (ToM).

3.3 WORKING MEMORY

Working memory is an elusive, multifaceted concept. Neuroscience and human psychology have proffered various definitions. Listing them or attempting to discuss the pros and cons of each would distract the attention of the reader from the real purpose of this short book. Further information is provided in the next chapter. It is enough here to quote the precise and informative words of Joaquín Fuster (2001): “...Working memory is emerging as a mechanism of temporal integration essentially based on the concurrent and recurrent activation of cell-assemblies in long-term memory networks of frontal and posterior cortex”. Fuster (2015, p. 6) points out that working memory should not be regarded as being synonymous with short-term memory if the latter is taken to be “the precursor stage of long-term memory,” and considers that in a “unitary view of memory with a common cortical substrate... working memory is the temporary activation of *updated* long-term memory networks for organizing actions in the near term; this prospective aspect is essential to the definition of working memory” (Fuster 2015, p. 6).

A principal aim of this book is to explore the question of whether rigorous inquiry supports or casts doubt on claims that tool-making abilities of great apes are commensurable with those reflected in stone tools made by hominins during the Late Pliocene and Early Pleistocene. Critical analysis finds the claims to be overstated because they appeal to

superficial technological aspects far more than to considered argument over the cognitive demands needed for making tools. An essential cognitive requirement for making a tool to serve a specific function is that prospective aspect of working memory which permits temporary activation of updated long-term memory networks for organizing actions in the near term. In plain words, working a stone substrate in order to produce an implement with specific desirable features requires the generation of a mental image of the final intended product, as well as the capacities both to retain it actively for continual comparison with the visual image of the current state of the substrate, and to exert ongoing behavioral corrections whenever the two images diverge.

Given the importance of working memory in tool-making, it is appropriate to consider briefly some studies on the working memory capacities of the great apes. A much-publicized comparative inquiry into the working memories of chimpanzees and humans involved a “limited-hold memory task” (Inoue and Matsuzawa 2007), modified from that which had been developed at the Primate Research Institute of Kyoto University, and in which chimpanzees touched numerals 1–9 in ascending order on a screen. In the modified task, a white circle appeared on the screen at the start of each trial and after the subjects touched it several numerals lit up for 650, 430, or 210 ms (milliseconds), after which the numerals were replaced by square white masks. Subjects had to remember the positions occupied before masking by each of the numerals in order then to touch the squares in the appropriate ascending order. The memory was investigated of three chimpanzee mother-offspring pairs and nine adult humans. Whereas, on average, humans outperformed the best adult chimpanzee at all three hold intervals, their performance was identical to that of the best juvenile chimpanzee (called Ayumu) at the longest hold interval (650 ms), albeit significantly worse at the remaining 430 and 210 ms hold intervals. It was suggested that Ayumu’s superiority over human subjects might owe to an ability “reminiscent of the phenomenon known as ‘eidetic imagery’” (Inoue and Matsuzawa 2007). However, the notion of “eidetic imagery” (Jaensch 1930) has long been viewed skeptically (Gray and Gummernan 1975). In any case, if, as supporters of the notion aver, “eidetic imagery” declines from childhood to adulthood, then, surely, Ayumu’s performance ought to have been tested against that of children, not only with that of adults.

Another serious methodological shortcoming was that the chimpanzees and humans were exposed to very unequal levels of training. Ayumu's alleged superiority disappeared when adult humans were allowed some training (Cook and Wilson 2010; Silberberg and Kearns 2009). Ayumu's performance was matched after they had received intensive time–pressure training at the latency of 210 ms (Silberberg and Kearns 2009) where the respective performances had differed most in the Kyoto study. In that study, however, Ayumu had lacked prior training at that latency; indeed, because it had been reported that, on average, Ayumu had spent 650 ms before responding, it remained unclear how much light was shed on the matter of Ayumu's superiority by the training of the human participants in the 2009 replication study. The matter was clarified when the training and test conditions to which Ayumu had been subjected were replicated precisely (Cook and Wilson 2010) by giving the original task to two adult humans who had been trained, as intensively as Ayumu had been, with the longest latency of 650 ms, after which their results with the 210 ms test out-performed those of Ayumu. Decay in performance when disappearance of the digits was followed by masking might implicate merely uncontroversial effects of iconic memory or retinal after-images, rather than “eidetic imagery”, and the appropriateness has been questioned (Cook and Wilson 2010) of the mask control condition that was intended to discard the retinal after-image explanation in the Japanese study. Given that synesthesia associations in humans can occur between colors and elements of well-learned series (numbers, days of the week, letters of the alphabet, and so on), it has been suggested, furthermore, that lengthy training in chimpanzees might have led to associations of numbers with colors, and that retinal after-images of colors could have been retained after colored numerals on the screen had been replaced by masks (Humphrey 2012). In short, there is no clear-cut evidence that Ayumu possesses a remarkable working memory.

A different approach to comparing working memory in humans, chimpanzees, orangutans, and monkeys used a computer version of a well-known children's card-game that involves detection of matches as cards are turned over (Washburn et al. 2007). When a joystick placed the cursor over a card the image that it concealed was revealed, and subjects then had to memorize that image in order to be able subsequently to identify a matching image that another card concealed, and thereby to obtain a reward. Increasing from two to six the number of different pairs of images, on cards to be matched, rendered the task more

and more difficult. Four experiments were undertaken. Three differed only in the types of image that the cards concealed: clip art in the first experiment, dot-patterns in the second, and lexigrams in the third. The fourth, undertaken only with humans, used clip-art images, with addition of articulatory suppression. Humans performed significantly better than monkeys and great apes in all experiments. Rhesus monkeys never performed above chance level, and, indeed, in the first experiment they performed significantly worse than expected by chance. Chimpanzees performed above chance level in the first experiment and in the third when presented lexigrams with which they had some prior acquaintance. Performance of great apes was affected more adversely by the level of difficulty of the task than was human performance: with three different pairs of images to be matched chimpanzees made four times more mistakes than humans, and ten times as many with four different pairs. In the second experiment, which used dot-patterns, the results of both great apes and humans were worse than in the first (whereas this was not so for the monkeys). Human performance in the first experiment worsened with added articulatory suppression, when the number of errors doubled, which was rather surprising given that the clip-art images did not correspond to known objects capable of being named verbally, and that verbal utterance was not necessary in order to solve the task; it was suggested, therefore, that language may have helped to link the “where” and the “what” of the task, and thereby to recall the locations of the concealed images. The study supports the view that there are significant differences between human visuospatial working memory and that of great apes and monkeys.

In a revision of the literature comparing working-memory abilities of human and nonhuman animals Carruthers (2013) classified abilities that draw on working memory in terms of ascending cognitive demands from levels 1 to 8. Of interest here are aspects referable to nonhuman Primates. Level 2 includes the capacity to hold more than two chunks of information temporarily in working memory, which traditionally is attributed to humans alone, on the notional basis of assigning to working memory a function to sustain pure memory (instead of the “fatidic” number 7 of Miller 1956). Carruthers cited a study in which macaques, required to memorize numbers in sequential order, succeeded in remembering up to three numbers (Botvinick et al. 2009), which is above the limits of working memory usually ascribed to nonhuman animals. In discourse about a pure-memory-sustaining function of working memory,

covert mental rehearsal and informational chunking must be discarded. Here, however, this cannot be done, because the monkeys might have performed mental rehearsal of their planned movements.

Another study (Hauser et al. 2000) showed that rhesus monkeys were able to distinguish between containers that hold two versus three items, and three versus four items, which would move the level of the pure-memory-sustaining function of the WM from two to four chunks of information. In a similar task, great apes were shown to be able to discriminate sequential comparisons beyond four, and their superiority of performance was interpreted by proposing the existence of an analogical system for estimating quantities (Hanus and Call 2007). Carruthers' revision supports the view that nonhuman Primates are capable of mental rehearsal of actions, occupying level 5 of his rating of working memory complexity. In support of this, he cited studies that include both anecdotal observations with chimpanzees (Osvath 2009) as well as controlled studies conducted with captive great apes which would indicate complex planning abilities (Mulcahy and Call 2006; Osvath and Osvath 2008). As will be discussed in detail below, most studies that claim to have demonstrated abilities of complex planning admit alternative explanations that need not involve sophisticated planning. Whilst Carruthers' revision offers a way to rate working memory in terms of complexity, which is likely to be useful for future comparative studies, the wide range of different species and methodologies considered complicates the extraction of clear-cut incontrovertible conclusions.

A more conservative consideration of the working memory capacity of chimpanzees juxtaposed their nut-cracking behavior with developmental trajectories for working memory in *Homo sapiens* from birth to puberty (Read and Van der Leeuw 2008). Although nut-cracking requires chimpanzees to manipulate three objects (nut, anvil, hammer), in general their working memory seems to stay at around 2, given that one in four chimpanzees never learn this tool-using behavior despite observing proficient conspecifics. In humans, a short-term working memory of size 2 is present in 3–4 year-old children. This is the age at which chimpanzees begin to crack nuts. During the first 3 or 4 years of life the developmental trajectories of increasing working memory capacity in *Pan* and *Homo* can be regarded as being more or less comparable, whereas noteworthy divergence ensues thereafter.

3.4 LIMITS TO TOOL USE, TOOL-MAKING, PLANNING, AND FORESIGHT IN GREAT APES

Analytical inspection of sequences of stone-reduction (so-called *chaînes opératoires*) whereby early Paleolithic artifacts were made finds that often their preparation involved orderly manipulative knapping procedures. These imply hierarchical operational planning with mental representations of likely outcomes in terms of the affordances of the raw material and the manual procedures required, as well as awareness beforehand of where to find appropriate raw material with suitable physical properties, and how, when, and where to undertake knapping—and with what end in mind for deploying a knapped stone.

Although a captive orangutan was trained, through imitation, to knap a stone and remove a flake with which it cut a string thereby opening the trap-door of a container with food inside (Wright 1972), attempts to train captive bonobos to imitate, with precision and accuracy, humans flaking stones, and thereby to extract a flake to cut a string in order to gain access to a reward, have led to outcomes that by and large were less successful (Savage-Rumbaugh and Fields 2010; see also Schick et al. 1999; Toth et al. 1993). Modifying stones for use as tools seems to play little part in the behavior of great apes. Nevertheless, at a zoological park a chimpanzee was observed preparing, modifying, and caching stones for subsequent throwing displays several hours later when the park was opened to the public; interestingly, the animal was “calm during gathering or manufacturing of the ammunition, in contrast to the typically aroused state during displays” (Osvath 2009). As already remarked, modifying stones is an activity that has been observed in some wild catarrhine and platyrrhine monkeys. Nevertheless, nonhuman Primates in the wild do not modify a stone in order to use it for modifying another object that is then used as a tool.

The use of wild chimpanzees of up to five sticks, each with different characteristics, as tools for extracting honey from hives of wild bees depends for success on using them in a particular order of relative rigidity (Brewer and McGrew 1990; Boesch et al. 2009), thereby demonstrating orderly hierarchical behavior. Again, observation of spatial deployment in wild chimpanzees during foraging implies a capacity to plan aspects of their behavior: thus, “Female chimpanzees ($n = 5$) were found to leave their sleeping nests earlier (often before sunrise when the forest is still dark) when breakfasting on very ephemeral fruits (figs),

especially when they were farther away. Moreover, the females positioned their sleeping nests more in the direction of the next day's breakfast sites with ephemeral fruit compared with breakfast sites with other fruit" (Jaanmat et al. 2014). This suggests chimpanzees can plan their daily routines flexibly, guided by whatever they anticipate or foresee that the next day may well hold out for them.

A related study attributes comparable planning abilities to wild Sumatran flanged orangutans (Van Schaik et al. 2013). Long calls emitted spontaneously by males predict their travel route. The trajectory they follow after one of these calls does not deviate much from the direction of the call. Moreover, if they are to change course after emitting one of these long calls they are likely to produce another call which is more predictive of the new direction to follow. When male orangutans emit one of these calls shortly before nightfall, next day they travel in the direction of the overnight call. When the positions of other males and females are registered after each of these calls conspecific males are found to distance themselves often from the flanged male trajectory, whereas females seem to do the opposite and stay closer to the travel route of the flanged male orangutan. The observations are interpreted in terms of attributing to the flanged males communicative intentions such that their calls inform other males of their travel plans so that these keep their distance while at the time they indicate to females the direction in which they are heading so that they can stay close to the males and benefit from their protective authority. It is even implied that the flanged males not only communicate the direction they will take but also do so a day in advance of embarking on it.

However, an alternative interpretation of the observations, which is both possible and plausible, does not involve any communicative intention. Flanged males may have come to learn from experience that emitting calls in a specific direction helps to keep the path clear from male competitors at the time when females are attracted, so they emit calls from time to time. They need not intend to communicate anything specific, such as where they are heading, let alone that "tomorrow" they will follow this or that route. Neither do the other males need to decode any propositional message in terms of whether the flanged male is going here or there, now or tomorrow; they need only try to keep their distance from the caller. It must be pointed out that getting away from a stronger male call or approaching it does not require either any understanding of the message or any specific route calculation; it is enough to have experienced "unsavory" encounters with bigger males in the past,

and to be able to calculate the direction of the sound, which is something that they can do easily thanks to their binaural hearing. Despite a claim that all of the animals involved in such a “putative” communication about travel direction possess and activate an episodic memory, it is unclear that the observations demand any such a conclusion to be drawn, and in any case the claim begs the question of how episodic memory is to be defined. Van Schaik et al. (2013) claimed that episodic memory has been found in a range of animals, yet what they reported is that some animals know where and when to find something, which constitutes necessary but not sufficient ingredients of episodic recall. Moreover, evidence of conscious recollection is lacking. It is, of course, difficult to demonstrate in the absence of language (Griffiths et al. 1999). In nonhuman animals, therefore, it is more prudent to refer to *episodic-like* memory than to episodic memory, though Suddendorf and Busby (2003) have argued convincingly that the most appropriate designation is What/Where/When memory (WWW-memory), reflecting Tulving (1972). Perhaps the most that can be inferred is that flanged male orangutans have a remarkable capacity for navigation in so far as they seem able to follow a specific route of travel for more than one day because the trajectory is maintained even after having stopped to spend the night.

Conjectural inferences, however plausible, must be treated with caution, because unknown factors might impinge on the observed behavior and thereby vitiate accommodative, self-justifying interpretations. Controlled laboratory experiments therefore are most necessary in order to assess capacities for foresight and planning in chimpanzees. It has been remarked in different contexts of psychological research that field observations often may “require external invalidity to test a prediction” (Mitchell 2012; see also Mook 1983).

Those capacities have been assessed with regard to tool-use in captive chimpanzees and orangutans (Mulcahy and Call 2006). Apes were offered eight objects of which only two were functionally suitable for obtaining a food reward. All were laid out on the floor of the testing room, where the apparatus that would contain the reward was fastened albeit blocked. The subjects could take as many tools as they wished before being ushered to a waiting room (1-hour delay) or to their sleeping room (14 hours delay). Once the subjects had abandoned the testing area, the tools left behind were removed. On returning to the testing room (1 or 14 hours later), the apparatus was baited and unblocked. Taken as a whole, the animals picked up more functional

tools than might have been anticipated were they to have chosen at random, as if they had anticipated their likely usefulness for solving a future task. In a control experiment, they were rewarded by returning with the suitable tools even when no apparatus was there for them to probe. Notwithstanding a possibility that uncontrolled environmental cues could have reminded them of the task ahead, the animals performed poorly because in fewer than half of the trials did the animals return with suitable tools to the testing room (except for a female orangutan).

Further research into the capacity of apes for self-control and forethought involved a deferred-gratification experiment (Osvath and Osvath 2008) in which two chimpanzees and an orangutan was shown a tray on which lay four tools, one of which was a tube. A handler gave a single preliminary demonstration of introducing tools through a hole in a box enclosing a plastic bottle containing fruit soup, enabling the outcomes to be seen; the box was then taken away. The animals were allowed to take one object from the tray and 70 minutes later the box was returned. Undoubtedly having seen how liquid could be sucked through the tube, nearly all the time they picked the tube for future use, ignoring unsuitable objects. Moreover, if a tempting grape was put in place of one of the latter, the apes nevertheless at first picked the tube, implying that an impulse to eat a tasty morcel was overcome by the ability to gain access to the even more enjoyable fruity liquid notwithstanding an obligatory long wait. Once they had ascertained the usefulness of the tube, in further trials they first ate the grape and then sucked on the tube. Between experiments, they were returned to the common ape enclosure with their tool, which they kept track of, and even protected from being grabbed by other occupants, whose behavior was an ever-present distraction. It was inferred that “apes preexperience the future tool function and its use” (Osvath and Osvath 2008). In a further experiment, they were shown also a tool that previously they had used to extract honey and might have been expected to elicit a positive response, yet it was rejected in favor of the tube, presumably having been assessed as unsuitable for sucking up fruit soup. The conclusions from the experiments have not gone unquestioned (see Suddendorf et al. 2009) and must be treated cautiously.

Does an ability of chimpanzees and orangutans to defer gratification demonstrate self-control enough to have enabled human forerunners to make Paleolithic tools? Deferment of barely an hour is hardly an impressive achievement in that regard. Perhaps longer experimental delays might afford more plausible conditions for addressing the question.

Nevertheless, guarding the tube from day to day seems to imply recognition of its usefulness and foresight of its likely future usefulness and possible deployment.

A study of “future oriented behavior” in great apes (Osvath and Persson 2013) involved testing their capacity to exchange a token to obtain a reward. Two orangutans and a chimpanzee learned to pick out from among four objects a bent strip of metal that they could exchange for an immediate food reward from their handler. Thus trained, they were put through experiment 1 that consisted of “one item forced selection”, in which they had to point to the metallic-strip token among the distractors in room 1 in order to be given it by experimenter 1, after which they had to wait fifteen minutes and then exchange it with experimenter 2 in room 2 in return for food: they successfully carried out the complex task. The experiment required them to discriminate between rooms and experimenters appropriate for the respective parts of the task, whilst at the same time the experimental design reduced possibilities of cueing, whether from the physical properties of room 1 or from the facial expression and behavior of experimenter 1. The reduction may not have been complete because the animals had taken part in earlier experiments involving exchange of tokens for food but it is unclear whether experimenter 1 had handed them those tokens: if so, that could have been a prior cue about their likely function; though that problem would not apply were experimenter 2 to have taken part in earlier experiments. Clarification of the possible methodological problem would be helpful, if only because analogous experiments had negative outcomes (Dufour and Sterck 2008); further research is desirable.

Research using a token-exchange task (Bourjade et al. 2014) was designed to show that great apes can plan flexibly for the future, without recourse to tools (in contrast to some previous studies, for instance, Mulcahy and Call 2006). Five bonobos, four chimpanzees, and four orangutans were trained to exchange tokens for food; there were three types of tokens and each subject was trained to exchange one specific type (its “valuable” token). Once the apes had exchanged their valuable token for a food item in consistent fashion, they proceeded to the test phase. This consisted of depositing 36 tokens (12 valuable tokens and 24 non-valuable “distractor” tokens) on the floor of a testing room (A). Subjects were allowed 10 minutes to collect these tokens and transport them into an adjacent room (B). Once the 10-minute period had ended, the subjects were ushered into room B, the door connecting rooms A

and B were closed, and any tokens left lying in room A were cleared away. The apes then were made to wait 20 minutes in room B before they were allowed into room A and asked to exchange any valuable tokens they had collected. In addition to the initial exchange condition, the experiment also included a release condition that differed from the exchange condition because after waiting for 20 minutes the apes were released without any exchange having taken place.

For each condition (exchange; release) 16 trials were run on 16 different days. Because exchange and release trials were not interspersed, subjects did not change condition until they had completed 16 trials. Half of the subjects faced first the exchange condition, while the other half faced the release condition first. The results showed that the total number of tokens brought back by bonobos and orangutans, but not chimpanzees, was significantly higher in the exchange condition compared with the release condition; which was regarded as evidence of flexible planning. Nevertheless, the results admit an alternative explanation. Any behavior that is immediately followed by the presentation of a reward (such as food) is reinforced thereby, which thus increases the likelihood of repetition of the behavior. During training, bringing back tokens was followed by the presentation of a food reward, implying that the behavior became increasingly more prepotent as training progressed. Later in the test, the behavior continued to produce the reward, increasing its prepotency further with repeated daily sessions (16 in all), though only in the exchange condition. The opposite occurred in the release condition, because a process of extinction developed in line with the diminution of reinforcement when tokens were returned repeatedly.

Although the total number of valuable tokens collected and exchanged in the exchange condition was greater than in the release condition, this need not imply flexible planning but simply may have been a consequence of a differential reinforcement schedule. Bourjade et al. (2014) argue against this associative explanation by saying that the learning curves do not seem to support a gradual increase or decrease in performance across trials for each of the conditions. Moreover, a long delay separates gathering the valuable tokens from being rewarded for bringing them back, rendering less likely an association between behavior and consequence. Nonetheless, the planning interpretation is not flawless. Were the condition (exchange versus release) to have been the cue that had informed the apes of the convenience of collecting and saving valuable tokens for future exchange, as Bourjade et al. (2014) seem to

imply, then selectivity would have been anticipated in the collection and transport of tokens, that is to say, a higher proportion of valuable tokens (compared to non-valuable tokens) collected and transported *only* in the exchange condition, yet no selectivity was observed as a function of condition, which may instead suggest that tokens were valued as secondary reinforcers, and not as means to secure the reward in a future exchange. The results, therefore, are open to alternative interpretation. Whichever explanation be preferred, it is still debatable that the study demonstrated flexible planning capacity, because the behavior that was intended to show so-called “flexible” planning is unspecific (bringing back more tokens across 16 consecutive testing sessions). It would have been more informative to have interspersed bouts of exchange trials with bouts of release trials in order to investigate whether the animals had adapted their behavior “flexibly” in an “on-going” way in order to maximize rewards obtainable in future exchanges. Furthermore, including specific contextual cues at the start of each trial, which signaled the opportunity for future exchange versus other cues signaling that there would be no exchange or even neutral cues that were uninformative, could have helped to make more specific predictions open to contrast with the observed behavior of the apes; which, in turn, could have helped to test whether or not the apes were planning flexibly with regard to their concepts of what might happen.

Planning abilities of four bonobos and eight orangutans were investigated (Tecwyn et al. 2013) by using a mechanical device (the operation of which did not require the use of tools) consisting of a Perspex paddle-box, containing eight rotatable paddles laid out on three levels, and with four possible goal locations at the base of the apparatus which could either be open or blocked. When open, any food reward that fell within could be recovered; when blocked, it could not. Each trial began with the experimenter positioning a piece of food over one of the paddles situated on either the first, second, or third levels of the apparatus. The apes were allowed to rotate the paddles using wooden handles. Each paddle was set up in one of three orientations (flat; diagonal left; diagonal right). If the food item was put on the first level, the apes only had to move the paddle right or left toward the marked goal location below. If it was put on the second level, they had to anticipate the direction in which the food would fall when they moved the baited paddle, after first orientating the lower level paddles and thereby clearing a path to guide so that the reward would fall all the way down to the goal.

If the food was put on the third level, they first had to orientate the paddles appropriately on the first and second levels before moving the baited paddle.

In 84.9% of trials for orangutans and 98.3% for bonobos, only the starting paddle was rotated, indicating that subjects ignored non-baited paddles and thus were unable to create an appropriate path thereby to guide the downward fall of the reward. Then the task was modified so that no planning ahead was required and the animal could resolve the task in a step-by-step manner; this was accomplished by preventing the food from dropping when the baited paddle was rotated, which allowed subjects first to position the baited paddle and then attend to paddles in the next levels until an uninterrupted downward path was achieved: now their performance showed improvement and was greater than chance. Altogether, the data show limited planning abilities in orangutans and bonobos in so far as subjects failed whenever they had to represent mentally and *anticipate* the consequences of their moves beforehand. The findings belie a view, drawn from observations on tool-use in the wild, that great apes have sophisticated planning abilities (Brewer and McGrew 1990; Boesch et al. 2009).

A study with another planning task gave seemingly different results (Völter and Call 2014). Two bonobos, seven chimpanzees, a gorilla, and two orangutans confronted a vertical maze consisting of a transparent box containing three horizontal levels across which ten gaps were distributed. At the start of each trial a food reward was placed in the uppermost part of the maze. The apes had to undertake manipulations in order to displace the food such that it passed through the gaps and could be retrieved by them from the lowest level of the maze. At various places in the maze three traps could be seen that blocked the path and the animals had to take them into account in order to devise a successful route for obtaining the food reward. The apes were able to plan one step ahead in order to avoid traps, and three apes even planned two steps ahead, which seems to attribute some planning ability to these apes, in apparent contrast to the findings of Tecwyn et al. (2013). Nevertheless, the task devised by Tecwyn et al. (2013) was a more stringent test of the planning ability of apes because, whereas the experiments of both Völter and Call (2014) and Tecwyn et al. (2013) required identification of an appropriate continuous path, in order for the food to get from the top to the bottom of the maze, in the study of Tecwyn et al. (2013) the apes, even *before* operating the top paddle,

had to envisage “mentally” how to rotate appropriately the two lower paddles in order to ensure continuity of a path that the food should follow. By contrast, in the experiment of Völter and Call (2014) all possible paths and their continuity within the maze were clearly visible and thus could be perceived by the subjects at the outset, therefore, they could track the paths visually before making any move. In the task designed by Tecwyn et al. (2013), the “right” paths were not visible at the outset, and the apes had first to envisage them by “mentally” rotating *all* the paddles beforehand; which laid heavy cognitive demands on their task and greatly increased the load on their working memory. Taken together, the findings of both studies reveal the fundamental limitations of great apes’ executive abilities and their capacities to envisage things that are not directly visible and to combine them in new and original ways. As will be discussed further in the next section, the limitations very likely impede great apes from making composite tools and using one tool to modify the properties of another by following a mental scheme to do so.

Another study (Bräuer and Call 2015) investigated whether tools for future use might be made by chimpanzees, bonobos, and orangutans. They were confronted by an apparatus comprising eight Plexiglas tubes (25 cm long, 3.5 cm in diameter) mounted next to each other in a battery placed perpendicular to the mesh of the subjects’ cage. The apes were provided with two soft wooden boards (12 cm wide, 8–10 cm long), and presented with the apparatus the tubes of which were baited with grapes. They learned to produce tools by breaking the wooden board into smaller pieces that they could insert into the tubes to dislodge grapes. Boards were short to prevent recovery of newly-broken fragments after insertion. The apes were provided with two wooden boards and allowed eight minutes to produce tools before the apparatus was unblocked, after which they could try to extract the grapes with them. Three baiting conditions were administered: no grapes, one grape, or eight grapes. The apes produced most tools in the third condition when eight tools were needed, though they had made fewer than two tools before then. They made tools mostly during testing, not beforehand. Their performance was unchanged when pressure on them was increased by reducing the latency of the tool-use phase from 120 to 50 seconds. The same number of tools was prepared regardless of the length of the tool-use phase. The apes failed to produce enough tools ahead of time, even when the substrate and baited apparatus were both

visible. Nor did they pay regard to time restrictions, which otherwise could have led to more tools being on hand for the shorter probing time. That they produced significantly more tools in the eight-grapes condition than in the no-grape or two-grapes conditions is taken as anticipatory fabrication, yet the apes needed to do no more than breaking the wooden board into smaller pieces. Simply breaking the board itself could have served as a distractor from the visible but unattainable reward (as has been reported in children in a deferred-gratification task: Peake et al. 2002).

An experiment about the possible capacity for foresight and prospective memory in chimpanzees, bonobo and orangutans (Martin-Ordas et al. 2010) involved a platform bearing three containers, one baited with frozen fruit juice, another with a less-preferred food (grape), with the third left unbaited, and five-minute and one-hour trials, corresponding to the lengths of delays between baiting and letting the apes choose to take from one of the containers. For five-minute trials, frozen juice and less-preferred food were available for grasping, whereas during the one-hour trial the frozen juice melted and only the less-preferred food was available for grasping. Four out of twelve apes (two bonobos, two chimpanzees, no orangutans) chose the frozen juice significantly more often than the grape after the short delay, and the grape after the long one. These results were interpreted as showing that those apes could retain the memory of, and thus predict, what was to be found where, and chose accordingly. Nevertheless, the results may not be altogether clear-cut and might admit a different interpretation. Taken as a group, the choices of the twelve apes were not *reversed* between five-minute and one-hour trials; rather, what was observed may have been only that desire for frozen juice waned after waiting for an hour whilst yet exceeding a desire for a grape. The results afford alternative plausible interpretations, namely (1) that a few individuals (two chimps and two bonobos) were able to recall and predict just *what* should be found *where* and *when* (an interpretation implying prospective memory, favored by the researchers); or (2) that the apes might have maintained a preference for frozen juice during both delay periods, though after one hour some failed to remember where the juice had been hidden and committed mistakes; this being an interpretation that need not imply prospective memory.

3.5 BLENDING REALITY AMONG DIFFERENT POTENTIAL SPHERES

Where preparation of a raw material to make a tool may hold out a possibility of two (or more) potential outcomes, depending on the sequential procedure of manual reduction of the raw material to be undertaken, meticulous attention has to be paid throughout the process, second by second, to the state of the object in relation to the anticipated outcome so that adjustments and corrections can be made in real time that favor its achievement, or maybe require its modification through a flexible behavioral strategy. Such executive capacity in modern people can be assessed by the Wisconsin Card Sorting Test (Berg 1948), though few comparable studies have evaluated the capacity in great apes owing to the difficulty of conducting commensurable tests on them, even in captivity. Nevertheless, a simplified version of the test has been applied to chimpanzee mother–infant pairs (Moriguchi et al. 2011). It was reduced to size versus shape, whereas the traditional test involved classifying cards by paying attention to three dimensions (shape, color, number) for each of which there could be four levels, namely, for shape, triangle, star, cross, or circle; for color, red, blue, green, or yellow; and for number, 1, 2, 3, or 4 elements. Even in the simplified version, the chimpanzees struggled both with forming classificatory criteria and maintaining these when reinforcement stimuli were altered. By contrast, five-year-old children have no difficulty in carrying out the task paying attention to all the dimensions and flexibly modifying the classificatory criteria.

Possible difficulties in undertaking such experiments on great apes can be side-stepped, in part, by appeal to an alternative approach employed in many studies of them, namely, exploration of their possible capacity for “theory of mind” (ToM), even though this usually is referred to the domain of social cognition rather than that of physical cognition. Nevertheless, there may well be a fundamental aspect common to both. This could be a capacity to maintain representations of alternative realities that may be distinctly different, juxtaposed or even seemingly incompatible: representations of not only what *is*, but also of what *will be* or what *could be* or *might be*. It may be the same capacity as that which underlies attributions of “false belief”, or which involves “perspective-taking at levels 1 and 2” and permits the blending of reality among different potential spheres.

When knapping a stone tool, for instance, representations may be envisaged of one or more possible outcomes, both desirable (“tools”) and undesirable (accidental “mistakes” and “waste” by-products), either of which may be affected by ongoing modification enabled by the flexible manual responses of a knapper from second to second. Multiple alternative representations require recruitment of cerebral circuitry in order to bear them in mind, whether “real” representations derived from perceptions, or imagined representations inferred from previously unfulfilled expectations, watching other knappers, or hearing their tales of woe, (or even half-remembered from dreams). To conclude, decomposing simple technology into distinct cognitive elements may help to evaluate the evolutionary implications of tool-use and tool-making in human and nonhuman anthropoids and the comparisons and contrasts between these.

Level 1 perspective-taking is the capacity to adopt visual perspectives of other individuals and to know what they can and cannot see. In an influential study of the mentalist abilities of great apes (Premack and Woodruff 1978), a female chimpanzee was the subject of experiments to investigate whether its responses showed its capacity to attribute mental states to its handlers who were shown in videos trying to solve a problem (such as reaching for a high-hanging banana) followed by stopping the video and showing two photographs of which one showed how to solve the problem and the other did not; because the first was chosen consistently, it was inferred that the chimpanzee was able to reason about the mental states of the handlers and divine their intentions.

Those experiments provided a basis for the development of a “knower-guesser” protocol, designed to find out whether a chimpanzee could adopt the visual perspective of a trainer. It had to discriminate between two trainers in order to receive or locate food hidden inside one of two containers; one trainer had seen where food was placed whereas the other did not know which container had the food: the chimpanzee had to make its choice based on the trainers’ visual knowledge (Povinelli and Eddy 1996). It had been trained to make a gesture to beg for food from one of the trainers. Whereas both trainers offered it food, the begging gesture could be seen by only one trainer, because the other had his back to the animal, had his head covered, or simply looked away. The chimpanzee made begging gestures regardless of whether the trainer could see it or not.

An experiment designed to find out whether chimpanzees could adopt the perspective of conspecifics was based on competition for food (Hare et al. 2000), in which the responses were studied in two animals, held

in separate cages, of which there were two cages without animals. Two equal amounts of food were made available, of which only one could be seen by both chimpanzees, because it was placed between the two empty cages, whereas the other was hidden from the view of the dominant chimpanzee behind a translucent screen within the empty cage nearest to the subordinate chimpanzee who therefore, unseen by the dominant animal, could gain preferential access to the food, whereas if, instead, a transparent screen was used the subordinate chimpanzee was denied an advantage of preferential access and desisted. Without entering into experimental details, suffice it to say that the trials could suggest that a chimpanzee may be able to adopt the visual perspective of another, particularly when these very social animals are *in competition* for a reward, with their cognitive capacities honed by natural selection to out-compete one another (see also Hare 2001). An attempt to reproduce the study met with less success (Karin-d'Arcy and Povinelli 2002), plausibly (Bräuer et al. 2007) because its spatial context had been so constrained as to favor an opportunistic tactic of rapid search-and-snatch over a strategy of first studying the opponent.

Face-to-face competition between a trainer and a chimpanzee for two pieces of banana (placed on the left- and right-hand side of a board) which the animal could try to grasp through a hole in the partition between them while the trainer tried to steal whichever the animal sought to grasp, was the object of situations in which the trainer paid greater attention to one piece than the other, or in which blinds prevented the trainer from seeing whether the animal was getting close to one piece but not to the other (Hare et al. 2006). Chimpanzees tried to grasp those pieces out of the trainer's sight, either because he had turned his back on them or because the blind hid them from his view. They even seemed able to take into account of whether blinds were translucent or transparent.

Matters of interpretation separate Povinelli's research team at Lafayette (see Povinelli 2000) from Tomasello's at Leipzig. Whereas the former appeals to a reading of the conduct of conspecifics (such as formation of associations, or learning rules such as not taking food in presence of a dominant individual), the latter considers that a principle of parsimony implies attributing mental states to other individuals in order to interpret variations in conduct when an animal competes with another for resources. Because attribution of particular mental states goes hand-in-glove with particular behaviors, it is well-nigh impossible to decide which interpretative approach is most appropriate.

The “goggles experiment” to test between them (Heyes 1998) is designed to investigate whether a subject, based on its own experience, might attribute mental states to others without their undertaking different behavior: animals are trained with mirrored goggles differing only in rim color though when wearing them subjects receive one experience as translucent (opaque) and the other as transparent; in the test phase, two experimenters wear the goggles such that one can see whereas the other cannot, and chimps choose which one to beg for food.

The goggles experiment has been used to investigate visual perspective-taking in chimpanzees (Karg et al. 2015). Chimpanzees were made familiar with two masks that differed only in rim color (yellow versus blue). While the yellow-rimmed mask was transparent the blue one was opaque. Chimpanzees gained experience with the properties of one mask type for 8 minutes; on the next day, they would experience the other mask type. Once they were familiar with the mask properties the experimenter put on one of the two masks and turned his head in a specific direction to see whether chimpanzees followed his gaze, as they are known to look in the direction toward which another individual is visually orientated. No difference was observed in chimpanzees’ gaze-following behavior toward the experimenter who was wearing a mask, depending on whether they had experienced that the mask was opaque or transparent, previously. Therefore, there was no evidence that chimpanzees in this study used their own visual experience to infer what another can see. In contrast, 18-month old infants followed the gaze of a blind-folded experimenter more when they had experienced see-through masks but not opaque blind-folds (Meltzoff and Brooks 2008). A previous study on gaze-following found that chimpanzees and bonobos, and to a lesser extent gorillas also, though not orangutans, followed an experimenter’s gaze more frequently when that was directed toward a barrier containing an opaque or translucent window, beyond which, and within the ape’s line of sight, a target was present sometimes and not at others, than when that barrier was replaced by a blank and windowless one toward which the experimenter gazed in the same direction as before (Okamoto-Barth et al. 2007). Chimpanzees and bonobos seemed not only to co-orientate their gaze with that of the experimenter, but also to take into account what the latter could or could not see. These results are in contradiction with the mask study described above.

Skepticism not having been assuaged entirely by the results of the masking experiment, a further experiment was undertaken that was a

variation of the mask one, which entailed competition over food with a human experimenter, in order to find out whether chimps fared better in competitive situations (see also Hare 2001). Subjects gathered experience with three different lids that could be transparent, opaque, or screened. Screened and opaque lids looked the same from the outside, though the screened version allowed objects to be seen that were placed below it. A chimpanzee sitting face-to-face with a trainer had to choose between stealing a peanut from under two lids; one was always opaque, and the other was either transparent or screened, ostensibly similar to the opaque one though the trainer could see through it. The trainer removed the peanut as soon as the chimp tried to grab it. The comparison was made between choosing the opaque lid (the trainer could not see the chimpanzee reaching) versus the transparent or screened version (that allowed the trainer to see the animal reaching), as a function of whether it was a social condition (the trainer was there to steal the peanut) or a nonsocial one (the chimpanzee was alone). It was found that chimpanzees preferred to steal the food from under the opaque lid more often in the social condition than in the nonsocial condition. This was taken to support their perspective-taking capacity.

Nevertheless, in the social condition chimpanzees still tried to steal food from under the transparent and screened lids in more than 40% of trials. This is disconcerting, because there were no additional derived costs from stealing the food from under the opaque lid, nor was there a higher reward waiting under the transparent or screened lids. Therefore, why should they risk losing the peanut while attempting to steal it from under the risky transparent and screened lids? If they could tell reliably, on the basis of their own experience, what the experimenter could or could not see, we hardly should expect any transparent or screened-lid stealing attempts. The experiment does not seem to have put an end to the debate about the visual perspective-taking abilities of chimpanzees which separate the Leipzig from the Lafayette researchers.

Level 2 perspective-taking refers to a higher-level understanding of perspectives: understanding that the same object might appear differently from another perspective (Flavell 1977). It involves both inferring what another individual can see or not from his position, and the form he attributes to it. If it is asymmetrical it can appear differently depending on the position of the observer. Humans achieve mental representations of different forms that a given object may take, without jeopardizing its recognition. Likewise, I can imagine how what I now see might appear to another.

Do chimpanzees have that ability? In an experiment involving competition between chimpanzees for food rewards (Karg et al. 2016) a sliding table was set up between two enclosures such that a subject and its competitor could sit opposite each other and the experimenter could move the sliding table back and forth between them. In the middle, an opaque vertical screen had two identical bread-sticks attached to one side of it such that they projected above it, but the competitor could only see what projected above the screen. Elastic straps on the side toward the subject allowed the height of the bread-sticks to be adjusted; the subject could see those to be of equal length. Notwithstanding having seen the bread-sticks before the experimental situation was set up, the competitor no longer knew the bread-sticks were still of equal length, and when the sliding table has moved the lengths of the visible parts of the bread-sticks appeared to change differently. The first subject had to indicate which of the two it desired. Before it was given any, however, the researcher moved the sliding table so that the competitor could choose; in other words, the first subject could receive a bread-stick only if it was able to anticipate what its competitor might choose, so that it would then choose the other piece. If the subject possessed level 2 visual perspective, then it might be anticipated that it would choose the one that had appeared to be longer to its “greedy” competitor, in full knowledge that the one that it first had indicated, which looked shorter from the other individual’s perspective, would be available when the table slid back toward the subject. This indeed occurred. However, in the absence of a competitor, the subject chose the bread-stick that had appeared to be the shorter from the viewpoint of the erstwhile competitor. Subsequent tweaking of the experimental conditions failed to resolve the methodological problem.

It is far from clear that this ingenious experiment showed conclusively that chimpanzees possess level 2 perspective-taking ability, and thereby, the capacity to complete a mental image of an incomplete object, rather than simply an awareness of the permanence of an apparently changing object. Level 1 perspective-taking alone could well explain the findings if what the subject was judging was whether the competitor could or could not see the *whole* of the object. The experiment therefore might be comparable to those tests of level 1 visual perspective-taking in which the part played by obstacles or barriers in a subject’s line of sight or gaze determines what can or cannot be seen, without necessarily implying that the subject has a mental image of the form in which the competitor sees an object that both can see in its entirety (not in fragments, as the bread

sticks were) albeit from different angles of sight and consequently with different forms. (Perhaps the experiment could be modified by employing asymmetrical objects that whilst being equal in size appear larger or smaller from the viewpoint of the competitor; or perhaps by using a magnifying glass in order to exaggerate the apparent size of one of the bread-sticks).

The capacity for entertaining false-belief is another aspect of the cognitive versatility that is needed for representing to a stone-knapper the intended outcome of his work in hand (literally, as well as figuratively!). Attribution of a belief to an individual differs from the attribution of knowledge because the belief need not correspond to a real state of affairs; it can require different or even contradictory representations to be kept in mind. Just as in the appropriate knapping of a stone tool, it is necessary, so to speak, to blend reality among different potential spheres.

Most commonly-used experimental protocols with great apes, when studying attribution of belief, tend to be of one of two kinds: namely, *cooperative* bait-and-switch (or change-of-location) experiments that investigate their capacity to communicate with a researcher by gesturing in order to locate food hidden in one of two containers; or *competitive* bait-and-switch (or change-of-location) experiments in which a subject in competition for a food reward with a conspecific has to outwit the latter's erroneous knowledge (false-belief). In one cooperative bait-and-switch experiment (Call and Tomasello 1999) apes watched while an experimenter hid a piece of food (bait) under one of two containers placed behind a screen that prevented them from seeing which container hid the food, whereas a second researcher (the communicator) standing beside the first had seen where the food was hidden. After removing the screen, so that apes could see the containers, the communicator placed a marker on the one with the food. Each ape was allowed to choose one of the containers; the apes (seven chimpanzees; two orangutans) learned to choose the marked container, thereby gaining the coveted reward.

In a subsequent false-belief experiment, the communicator was again visible to the ape which watched the baiting process from behind a screen that then was removed. This time, however, the communicator turned his back on the containers before marking one of them. The first experimenter then switched the location of the containers in full view of the ape but not of the communicator. The communicator then turned around and marked the container at the place, where the baiting had been witnessed beforehand. Were the apes to have been capable

of attributing beliefs to the communicator they should have understood that, in the false-belief test condition, the communicator would have marked the container (in the same way as during the training trials) in which the food was last seen to have been hidden, and hence where the communicator believed the food to be hidden still, even though it was now under the other container owing to the switch of the containers by the first experimenter. Were they to have understood the test situation in those terms (that is to say, of false-belief), the apes should have been expected to choose the unmarked (baited) container, whereas in fact they usually chose the marked (that is to say, empty) container over the unmarked (baited) one.

In a competitive bait-and-switch experiment (Kaminski et al. 2008), with the aim of assessing whether apes could exploit a capacity to attribute false-belief in order to out-compete conspecifics (see also, experiments on visual perspective-taking: Hare 2001), food rewards were shown first to two apes who then were sat on opposite sides of a sliding table. They then engaged in a back-and-forth task in which subject and competitor took turns in choosing from a row of three opaque containers, two of which were baited by the experimenter in front of the subject which therefore also could see which container was left empty, whereas the competitor saw only one baited container. The table was slid toward to the competitor in order for the latter's choice to be out of sight of the subject. The table then was slid toward the subject. Subjects preferred to select that container the baiting of which had not been seen by their competitor, thereby implying that they could attribute knowledge to their competitor about where food was likely to be found. In the false-belief attribution task, two different kinds of food, differing in their attractiveness to apes, were used as baits in the containers. Subjects saw the experimenter mislead their competitor by placing especially appealing food in one container before moving it to another while their competitor's view was blocked. They then had to predict their competitor's choice of the incorrect container, based on its false-belief that the preferred food still lay hidden inside it. Subjects avoided choosing the one containing their preferred food, plausibly reflecting a "Machiavellian" calculation of short-term deferred gratification while their competitor chose the one they had feigned to ignore. They alone had witnessed the changed position of the especially desirable food, and by having feigned disinterest were able, unchallenged, to lay claim to the container that concealed it.

Inconclusive findings resulted from a different bait-and-switch experiment (Krachun et al. 2010). Its basic concept was neither communicative-cooperative nor competitive. Chimpanzees watched a handler (the baiter) putting grapes or bananas into a small container of a particular color (yellow) before closing its lid and covering it such that if the bait was grape the cover was of one color (blue) whereas if it was banana the cover had a different color (white). After observing all that, chimpanzees had to choose a cover. Five out of six of them learnt to choose the white cover if they had seen the handler put banana into a yellow container, or the blue cover if they had seen grape being put into the yellow container. The subsequent experiments tested the animals for false—as against true-beliefs. In a test for false-belief, the chimpanzees watched the handler putting bait, as before, into a container and closing it. The handler then went away and was replaced by another researcher who, watched by the animals, switched the bait in the container, such that banana was substituted for grape or vice versa, whereas the colored cover stayed the same as before. The handler (baiter), who had not seen the switch, then came back. A screen was set up in front of the chimpanzee such that it was unable to see the handler put a blue cover over the yellow container in the mistaken (false) belief that it contained grape; on the removal of the screen, the animal had to choose a cover. The next stage of the experiment tested for true-belief. Now the baiter stayed and watched the researcher carry out the switch. It was argued that if the baiter's false-belief about what was inside the yellow container had been recognized by the animals, then they would choose the colored cover corresponding to the type of bait first put by the baiter into the yellow container, over the alternative cover. In like vein, were the animals to have grasped that the baiter in the true-belief trial was correct (having seen the switch) about what now was inside the yellow container, then the expectation ought to be that the cover would be chosen which corresponded to what in fact was in the container under it, rather than to what the baiter had put into the container initially. Despite the finding that the chimpanzees tended to choose the cover according to what really was within the container, there nevertheless is room for a simpler explanation than that the animals had grasped the baiter's awareness of the situation and had behaved in consequence: the simpler explanation is that they merely had learnt a rule to "choose based on the current contents of the yellow container" (Krachun et al. 2010), implying an acquisition of knowledge by learning that does not require attribution of belief to another individual.

Better results were claimed from a cooperative bait-and-switch study that used a mechanical-like apparatus instead of more traditional containers (O'Connell and Dunbar 2003). A chimpanzee was trained to use the situation of a peg, on a box-like apparatus, in order to identify a baited drawer among a row of four drawers set within the apparatus. The peg itself was fastened to a fan-belt, and its situation (relative to drawers below it) could be changed by turning a crank-handle behind the apparatus so as to move the belt. The ape watched while the researcher, with food in hand, placed the peg above one of the drawers. From behind the apparatus, the food was then placed inside the drawer marked by the peg. The researcher then reappeared and pushed the apparatus toward the ape which chose a drawer by pointing at it. Once it had learnt to choose the drawer below the peg, and had been rewarded for so doing by receiving the contained food, the ape was subjected to randomly alternating false—and true-belief test trials. In the former, it watched while a researcher placed the peg over a drawer and then went behind the apparatus in order to bait the drawer again. With the researcher behind the apparatus, occupied with baiting the drawer, the ape now saw the peg move to a new position directly over a different drawer. In fact, the researcher had turned the crank-handle behind the apparatus, moving the peg on the belt to a new situation. The researcher did not return to the front of the apparatus, where the new situation of the peg could be seen, but instead carried on with the baiting process. In this false-belief test, the researcher did not see that new position of the peg until the baiting process had been completed. More often than were to have been expected by chance, the chimpanzee selected the previously marked drawer in false-belief test trials and the newly marked drawer in true-belief test trials. It seemed to be capable of attributing beliefs at the level of a four-year-old child. Nevertheless, its performance could be explained just as well in terms of having learnt from the training sessions to choose that drawer toward which the researcher last had a direct line of gaze to the peg above it, rather than, otherwise, having learnt to choose the drawer last seen by the researcher and which therefore might be believed to be the one under the peg. A nonmentalistic interpretation suffices to explain the findings.

Demonstration of the capacity of great apes (seven chimpanzees; four bonobos; four orangutans) to attribute false beliefs to others has been claimed (Krupenye et al. 2016). An anticipatory looking paradigm was used (previously employed with positive results in two-year-old children: Southgate et al. 2007), in which the apes witnessed on a television

screen agonistic encounters between a human experimenter (actor) and a “so-called King Kong (KK) character” (another human experimenter disguised in a KK costume). The reason for introducing this unusual character is explained by asserting that “To encourage subjects’ engagement, we presented simulated agonistic encounters between a human (actor) and King Kong (KK), an unreal ape-like character unfamiliar to the subjects.” (If the use of this half-human half-ape character was meant to disguise the identity of one of the experimenters from the apes, then it is unclear why the other experimenter was treated differently.) The main procedure was that in the false-belief task a human (our actor) was “attacked” by the KK character, who afterwards hid in one of two haystacks but then moved to hide in the other after the human actor entered the zoo building to search for a weapon “stick”. Therefore, when the human actor returned with his stick and searched for the hidden KK, it was expected that the ape whose capacity to attribute belief was being investigated, with its gaze monitored, should look first toward the hiding place in which KK was last seen by the human actor, anticipating that the human would search for KK driven by his false belief. In a different false belief experiment, more similar to the classical bait-and-switch paradigm, a human experimenter and KK “fought” over a stone. The human experimenter hid a stone below one of two containers. In the false-belief test, the stone was moved to the other container by the “nasty” KK while the human experimenter was outside the room. Upon returning to the room, the human experimenter was expected to search for the stone in the first container, where he wrongly assumed the stone to be. Again, the gaze was monitored of an ape watching the sequence of events. In both of the experimental situations, the apes’ first looked to where the human actor had last seen either KK or the stone being hidden: this was interpreted as the capacity to attribute false belief to third parties. An important effort has been made to rule out some alternative lower level explanations. For instance, the KK and the stone were removed entirely from the scene after the second hiding, in order to avoid the possibility that, on the return of the human actor, their presence might attract the gaze of the ape under investigation.

Not having food hidden discounts a possibility that the gaze of the ape whose belief attribution is under investigation were driven (biased) by a desire for the food, instead of the agent’s beliefs about its location. However, it may be wondered whether the apes whose belief attribution is being investigated understood the situations enacted by the KK character and the human actor, in the same way as we humans do. In

the first place, the situations are odd. KK neither resembles a human nor yet behaves like a real ape. In the agonistic fight involving the use of a stick the ape under investigation had to keep track of innumerable events and attribute complex intentions to the characters (for instance, revenge from a previous attack). Moreover, a fight over a rock between a KK ape and a human experimenter can hardly be called a natural situation. The KK-human actor interactions are complex, involving both intention and goal-attribution in a rather artificial situation as the apes have to infer that the subjects are fighting over something that unlike food has no meaning for them, and therefore complicate the investigation of belief-attribution. The researchers assume that the apes have understood all of the complex interactions and, therefore, that the first gaze monitored was a reliable indicator of false-belief attribution. However, a general rule of the type “agents search for things where they last saw them” (see also Perner and Ruffman 2005) could satisfactorily explain the results without a need to imply the ability to attribute belief. This lower level explanation was discounted on the grounds that, because previous studies had demonstrated complex “theory of mind” (ToM) abilities in great apes, a mentalistic explanation seemed more fitting, adducing, in support, other findings from the researchers’ laboratory (Karg et al. 2015). Awkwardly, however, in that study the apes had failed to follow the gaze of an experimenter wearing a mask, regardless of their acquired knowledge about the visibility properties of the mask, in clear contrast to 18-month-old babies who pass this perspective-taking test (Meltzoff and Brooks 2008); and when the procedure was changed, in order to foster competition, the apes’ performance was far from proficient, some improvement notwithstanding. The reason for choosing a mentalistic over a rule-guided interpretation of a specific experiment should not be determined by results from related experiments, otherwise there would be no need to put to the test any specific cognitive ability. Moreover, a seemingly simpler ToM ability, such as level-1 perspective-taking stills eludes conclusive demonstration; results are mixed and therefore open to interpretation, and only a failed attempt to demonstrate level-2 perspective-taking in great apes can be reported. The study is a valuable first step of many that will have to be taken on a long, winding road toward reliably and definitively demonstrating false-belief attribution in great apes. Clearly, there are unresolved methodological problems about designing appropriate experimental protocols for investigating the matter (see Lurz 2011).

Moving somewhat away from the matter of perspective-taking and belief-attribution, it is worth considering the results of experiments designed to gauge the ability of great apes to make choices and plan their use of tools, which indicate their difficulties in maintaining and combining simultaneous disparate images of reality (Mulcahy et al. 2005), and imply differences from the early hominins who used and made stone tools. The apes confronted a food-retrieval task in which they had to use a stick-like tool to bring a grape within reach. In order to attain the out-of-reach grape, they had to choose one of two tools of a different length lying in parallel on a platform. In an initial experiment they could see both the tools and the reward, and therefore they could compare their distance from the food with the length of each tool in order to decide which one to choose. Next, the lengths of the two tools were changed, such that the shorter tool was long enough for the task: the apes chose at random when both tools were long enough to retrieve the grape, whereas they had preferred the longer tool when the other was too short for retrieval. Next, the tools had to be chosen in a different room from the one with the grape: now, the apes invariably chose the longer tool from pairs of whatever length, even when the shorter would have served. After that, they were given direct access to a short tool, and then shown a longer one and a grape both of which were out of reach. Now, the shorter tool was chosen when it served to retrieve the grape, but when it was too short it was used often to retrieve the inaccessible longer one with which the grape then could be obtained. They thus showed selectivity and planning abilities, organizing their behavior hierarchically according to the task demands (thereby increasing efficiency and reducing energy expenditure). Then, the experiment was repeated with the difference that the tools and grape were in separate rooms. Now the apes always preferred to use their accessible short tool to retrieve the inaccessible longer one before returning to the grape, even in those trials in which this was an unnecessary intermediate step, thereby incurring an additional cost in order always to secure the reward, which implies the ability to make appropriate decisions between alternative choices. This argument was the basis for a final experiment in which tools and grape were in separate rooms though with the difference that only one tool was available and therefore no choice was involved; now the apes refused more tools and undertook fewer attempts to retrieve the grape when the tool was too short.

Table 3.1 Afterthought: Suggestions for developing experiments into the capacity of great apes to make tools

What might be the cerebral requirements in order for an ape to respond to a specific need (such as a foraging problem) by creating a mental representation of an inexistent tool that might help it to satisfy that need? Could they be similar to cerebral requirements for mediating attribution of false-belief, given a similar need to represent not only things that are, but also things that might be or will be? This is not implausible. Perhaps, assembling composite tools requires, furthermore, a capability of especially precise manipulation of the different elements that must be put together.

An informative experiment here might be similar to that of Bräuer and Call (2015), though instead of requiring the animal to break a wooden board into smaller pieces for insertion into tubes in order to dislodge grapes, the apes might be provided with disparate elements that could be bound together to make a functional composite tool. Perhaps, they could be provided with pieces of board or other materials that can be attached to each other (possibly with magnets if the materials were metal) by simply manipulating them (to lessen a possibility of confusion related to the level of motor coordination/precision involved) and thus to produce a longer tool suitable for dislodging grapes in the tubes. Such an experiment might share aspects in common with human preparation of stone tools were the apes first to see the baited apparatus, and hence, the task requirements, before being moved to an adjacent room, where they would work with the disparate elements to put a functional tool together.

Another approach to examining the capability of apes to make tools for future use, requiring mental representation of an intended “tool to be,” which satisfies the task requirements and does not imply assembling disparate elements, might be one in which apes are presented in one room with several baited apparatuses that work differently, and therefore, the apes are required to produce different types of tools that have to be obtained from different substrates. The animals first might enter the room containing baited apparatus (beforehand they will have worked on each apparatus separately and produced appropriate tools reliably), after which they are taken to a different room where they will find the substrates to produce the tools needed to deal satisfactorily with different apparatuses. The methodological novelty introduced here is that the apes’ success cannot be linked to their production of functional tools by random manipulation of substrates, because they have both to represent mentally the different types of tool that they require, and to be able to choose the appropriate substrates needed to produce them. Success would demonstrate that they had represented mentally the task requirements as well as the tools-to-be that satisfied those, and thereafter had planned their behavior to put together the specific type of tool needed. By contrast, if all that is required to solve the task is to break a substrate into smaller pieces in front of a baited apparatus, then it is impossible to tell whether subjects broke the board because they were bored, or perhaps excited on seeing food, and in the process came to recognize that some of the newly produced pieces worked, or whether they knew what features the tools should have in order to work and then specifically produced tools that had those very features.

(continued)

Table 3.1 (continued)

The matter of considerably deferred gratification implied by careful knapping of Paleolithic stone tools for future use, together with the likelihood that early *Homo erectus* had cognitive capacity for envisaging the shapes of tools-to-be and some recourse to appropriate implicit long-term procedural memory of their preparation, as well as abilities both for observational learning of accurate and precise manual procedures and for correction of mistakes during knapping, all suggest the advisability of developing contrastive or comparative experiments with great apes in order to determine the limits of their capability to make tools by imitating, with precision and accuracy, a lengthy series of manual procedures performed by a trainer (perhaps involving 20 operations), in order to produce an accurate copy, and then to reproduce the same series of operations after increasingly longer intervals (days, weeks, months) in the absence of a human trainer. Perhaps, particularly coveted succulent food might then be produced as a reward for correct performance, in the absence of which only boring routine food would be available. Because orangutans are renowned for their manual dexterity and ingenuity, perhaps such experiments might best be undertaken with them.

The results of the study are most informative because they show that the apes were willing to incur additional energetic costs whenever tools and food could not be seen together, which seems to imply that their capacity to represent and compare food-distance with tool-length was limited. It is clear from the results of the final experiment that the apes showed a reasonably high degree of mental representation, yet this final experiment was less demanding than the preceding one, because they needed only to compare mentally the food-distance with the length of one tool, and not two as in the previous experiment. This experiment strengthens a view that the mental representation of apes is constrained and therefore limits the likelihood of their ability to envisage different alternative forms that a tool should take when making it. This view chimes with various arguments in support of attributing to Early Pleistocene *Homo* capacities for perspective-taking, mental time-travel, prospective thinking and “theory of mind”, alongside critical evaluation of the prevalent opinion that explicit memory exists in other mammalian taxa (Murray et al. 2017, esp. pp. 383–385) (Table 3.1).

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Early Tool-Making and the Evolution of Human Memory Systems in the Brain

Abstract Outlines about ancient Paleolithic artifacts and early *Homo* (2-1 Ma) skeletons precede considerations about cognitive versatility and developmental limitations of evolving brains. The adaptive behavior included technical skilfulness, reflected by artifact diversity, and manual dexterity requiring *backward* “haptic” touch memory, needed for habitual automatic, accurate handiwork, and *forward* “prospective” memory about foreseeably usable tools. Observational learning transmits skill insecurely, endangering persistence of evolutionary advantages. Their genetic or epigenetic underpinning enabled cerebral enlargement, affecting regions for different kinds of memory, imitation, language, and tool-use. Fundamental matters include imitative behavior and prefrontal and parietal mirror-neuron circuits, inferior parietal lobule tool-using specificity, long-term procedural memory and temporal lobe hippocampal-parahippocampal cortex, and working memory and neuronal haptic responses in prefrontal and parietal cortex. All underpin *human* capacities, whereby haptic working memory and propensity for habitual procedural memory evolved alongside explicit and implicit mental perspectives blending past and present behavioral memories into alternative behavioral concepts underlying Paleolithic diversity.

Keywords Pleistocene · Paleolithic · Stone-knapping · Alternative behavioral chains · Combinativity · Cerebral cortex · Myelination Prefrontal · Premotor · Parietal · Mirror-neuron · Temporal

Hippocampus · Haptic working Memory · Long-term memory
 Procedural memory · Prospective memory

4.1 A THUMBNAIL SKETCH OF SOME EARLY PALEOLITHIC TECHNOLOGICAL DEVELOPMENTS

Flaked stones and cut-marks on bone imply tool-making and tool-using activities around 3.4–3.3 Ma (million years ago) in East Africa (Harmand et al. 2015; Lewis and Harmand 2016; McPherron et al. 2010). Australopithecines (present in Africa since before 4 Ma) were probably responsible, given that the oldest skeletal remains assigned to *Homo*, found in Ethiopia, date from around 2.8 Ma (Villmoare et al. 2015) and 2.3 Ma (Kimbel et al. 1996), though only after 2 Ma are there indisputable remains of our genus at other East African sites. Numerous flaked stones and flakes date from around 2.5 Ma (Semaw et al. 1997; see also Harris 1986), and by 2 Ma, such “Oldowan” artifacts, including a few that show “secondary” knapping (or “retouch”) of a primary flake scar, are much in evidence at the eponymous type site and elsewhere in East Africa, where they could have been made by australopithecines and incipient *Homo* alike. Typical artifacts are pebble tools flaked on one surface, chopping tools flaked on opposing surfaces to produce a sharp edge, hammerstones, and flakes and fragments, of which a few were the object of secondary knapping, and several tools show signs of use or damage. At Olduvai, some stones were worked on rock taken from outcrops 8 km (5 miles) away, their suitability for the purpose undoubtedly having drawn the attention of hominids.

Analysis of sequences of Oldowan reduction of stone by inspecting and refitting pieces of stone that have been excavated reveals that knappers often had taken preferential advantage of affordances offered by those areas on a stone core which, when struck with a hammerstone, were conducive to ready removal of more than one flake or fragment because their shape offered a perpendicular or acute angle, thereby facilitating removals, especially from those types of stone rich in silica with a tendency to conchoidal fracturing (Roche 2005). It may be remarked that captive bonobos often fail to take advantage of such affordances, despite the earnest endeavors of their human knapping instructors. The neuroanatomical configuration of small hominid brains sufficed for such behavior although they were no bigger than bonobo brains. At several

sites, chopping tools and flakes are found among or beside remains of large herbivores, and primary access to their meat, fat, and marrow by hominids is inferred by many paleoanthropologists, some of whom conjecture that increasing carnivory impinged on the evolution of human morphology, with skeletal, dental, and developmental consequences, and perhaps neurological ones also.

By 1.8 Ma, *Homo* is found beyond Africa, namely, at Dmanisi in the Republic of Georgia, albeit with the Oldowan tool-kit, which may have aided dispersal. In Africa, two technological Paleolithic developments followed which are interesting from the standpoint of cognitive evolution in *Homo*. First, around 1.7 Ma, elongated stone artifacts appear (Asfaw et al. 1992; Beyene et al. 2013; Delagnes and Roche 2005; Lepre et al. 2011; Roche et al. 2003) that were flaked on two symmetrical opposite surfaces; these “bifacial” tools end in either a point when they are called “hand-axes” or a tranchet edge (“cleavers”); these large cutting tools are also found two or three hundred thousand years later on in the Near East and South Asia, and shortly after 1 Ma in Europe. There is microscopical evidence that such artifacts sometimes bear traces or residues from use with material derived from plants (Domínguez-Rodrigo et al. 2001) and animals (Solodenko et al. 2015). It should be mentioned, in passing, that perishable fashioned wooden spears are unknown, or have not survived, from times before 0.4 Ma, and that before 0.2 Ma, traces of evidence are lacking for composite hafted artifacts of stone with wooden shafts or bone handles (such as pitch adhering to a stone tool, or wear on a pointed stone consistent with erstwhile binding).

Secondly, by 1.3 Ma, artifacts appear, often disk-shaped, that were prepared bifacially, often seemingly less for use as tools themselves, than for regular removal, from their surfaces, of flakes for use as small tools (de la Torre et al. 2003), though this interpretation has been challenged (Díez-Martín et al. 2012). The two surfaces can be symmetrical or asymmetrical. In the latter case, they may reflect sequentially (“hierarchically”) differentiated operations undertaken to prepare one surface in a fashion that facilitated subsequent removal of a flake with a shape (for instance, oval, triangular, or oblong) that depended on how that surface had been prepared; such “Levallois” preparation characterizes many western Eurasian Paleolithic assemblages of the later Middle and early Late Pleistocene and permits a range of flake shapes, sometimes enabling recurrent removal from a core of two, three, or even four regularly

shaped flakes or flake-blades, often then knapped further by “secondary knapping” or “retouching.” All the same, evidence abounds of less structured (informal, expedient, or opportunistic) procedures by which stone artifacts were made by Pleistocene humans throughout the world during hundreds of thousands of years.

The matter to which particular attention is drawn here, however, is that because several assemblages from the later Early Pleistocene and Middle Pleistocene provide examples of large bifacial (“Acheulian”) cutting tools *together* with small tools prepared by discoidal or even “Levallois” procedures of stone reduction by recurrent knapping of a prepared surface, those assemblages testify to a capacity of their knappers to make *choices* between *alternative* chains of behavioral activity, each of which is the object of the knapper’s recognition (or “secondary cognition”) of its irreversibility once embarked upon. In other words, there is no possibility of backtracking in order to turn into an elongated pointed hand-axe a discoidal core that has been the object of recurrent knapping in such a way that one or more useful flakes can be struck from its prepared surface, whether by a “centripetal” blow aimed toward the center of that surface, or by striking it in ways that leave behind “orthogonal” flake scars side by side. The behavioral alternatives imply deferred gratification with regard to possible outcomes of uses to which the artifacts might be put. Furthermore, they imply a capacity to evaluate the advantages or otherwise of particular alternative self-generated procedural schemes of tool-making behavior *before* choosing to undertake either of them (or perhaps neither) (Figs. 4.1, 4.2, 4.3, 4.4, 4.5, 4.6, 4.7, 4.8).

Moreover, in addition to the fundamental cognitive aspect of what Piaget might have regarded as the knapper’s “logico-mathematical” awareness of possible *alternative* shapes to be prepared and the separate manual procedures appropriate for achieving very different outcomes (see also Wynn 1989), consideration also must be given to the sources of the knapper’s recognition of the alternative options in the context of what around 1.5 Ma undoubtedly was a social environment endowed with very limited linguistic fluency. In experiments with great apes, the experimenters can decide upon the alternatives to put before the animals. How, in the first place, did the alternatives come to the attention of, or become available to knappers, for a possibility to arise of their being in a situation to make any choice whatsoever? In this chicken-and-egg conundrum, how was the first egg hatched? Part of the answer could be that after about 6 Ma, when the evolutionary lineages of panins and

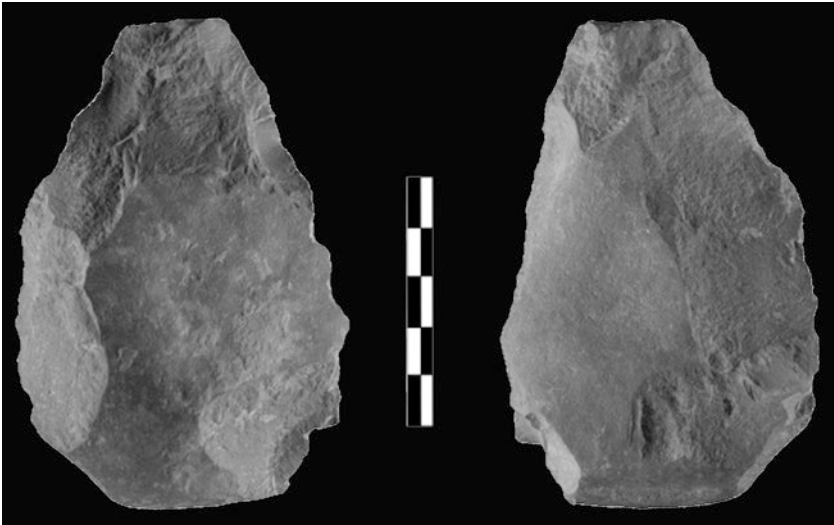
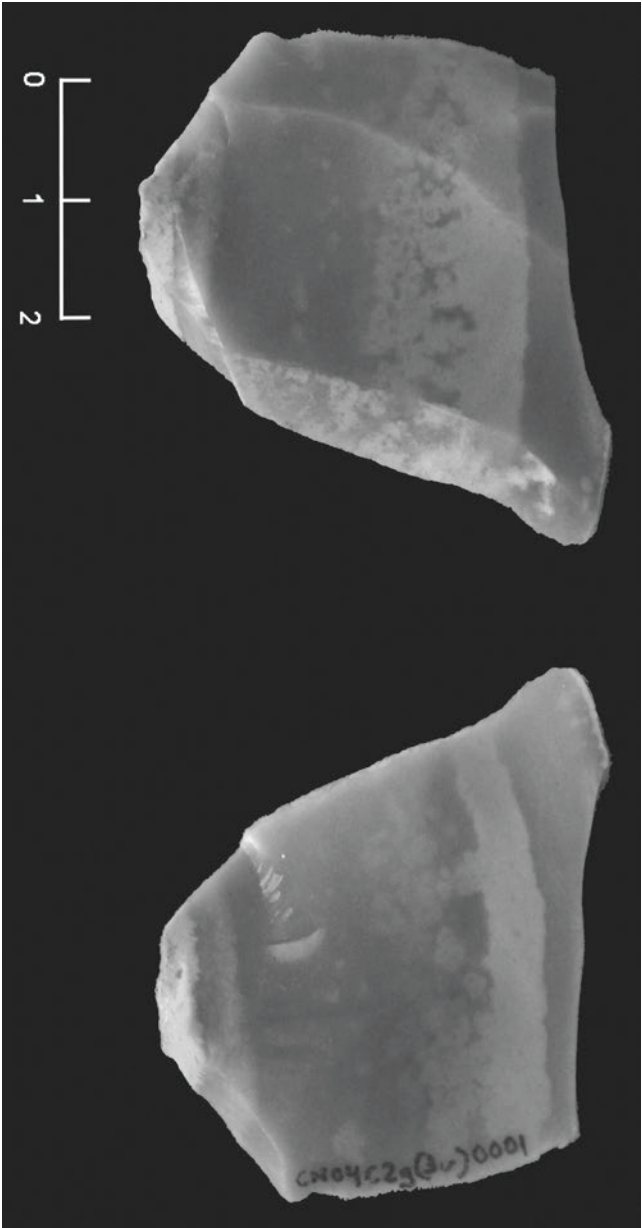


Fig. 4.1 Artifacts from Cueva Negra del Estrecho del Río Quípar, Murcia, Spain (reproduced with the permission of the Murcian Association for the Study of Palaeoanthropology and the Quaternary): bifacially flaked hand-axe on a flat limestone cobble

hominins parted company, there gradually developed in the latter a relatively greater capacity for working memory and mental recursion (Read 2006, 2008, 2017). It could be reflected in the appearance in the Late Pliocene and subsequent Pleistocene record of an increasingly wide range of Paleolithic artifacts (Read and Van der Leeuw 2008, 2015). We humans also have remarkable capacity for developing long-term memory and turning into automatic procedural memory and habits some links that we have learnt to associate between stimuli that at first we had perceived consciously (Berry and Dienes 1993) or even barely so (Reber 1989, 1996). Nevertheless, when salient novelties impinge, we modify procedural sequences, often seamlessly (think about steering and braking while pedaling a bicycle along a street, which is an activity children learn more by practice and experience than by once having sat through a talk about how cyclists should attend to the Highway Code). Returning to the matter of the very earliest Paleolithic artifacts on which flaking gave rise to a cutting edge, enough cognitive capacity already must have been



◀ **Fig. 4.2** Artifacts from Cueva Negra del Estrecho del Río Quípar, Murcia, Spain (reproduced with the permission of the Murcian Association for the Study of Palaeoanthropology and the Quaternary): flake struck by recurrent flaking of a prepared chert core; note facets on its striking platform (“heel”)

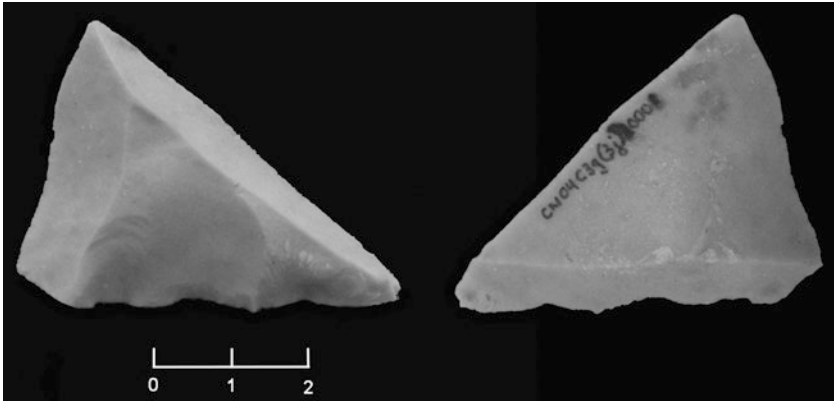


Fig. 4.3 Artifacts from Cueva Negra del Estrecho del Río Quípar, Murcia, Spain (reproduced with the permission of the Murcian Association for the Study of Palaeoanthropology and the Quaternary): flake struck by recurrent flaking of a prepared chert core

present in order to entertain a notion that a cutting edge could be an outcome of manual modification of a round pebble (Pigeot 1991). More was needed than evolution merely of short-term or working memory capacity.

4.2 REMEMBERING ALTERNATIVE COMBINATIONS AND THE EVOLUTION OF HUMAN BEHAVIOR

Preverbal human infants at play with physical objects seem to show “logico-mathematical” behavior, by constructing and deconstructing groups, and arranging and rearranging them in alternative sets or compositions, which has been interpreted as a cognitive capacity for *combinativity* (Langer 1980, 1981, 1986). Notwithstanding possibilities for impingement of silent cues from child-carers, these do not seem

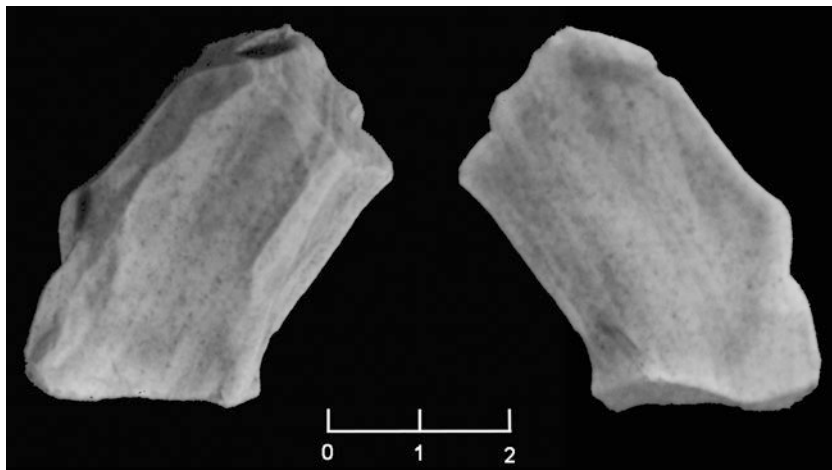


Fig. 4.4 Artifacts from Cueva Negra del Estrecho del Río Quípar, Murcia, Spain (reproduced with the permission of the Murcian Association for the Study of Palaeoanthropology and the Quaternary): flake struck by recurrent flaking of a prepared chert core

to have urged the infants toward particular behavioral outcomes, nor did they depend on reinforcement by rewards of food treats or drink. Moreover, decomposition of sets and rearrangement of their components into *alternative* ones seem to reflect a capacity for self-generation of imagined composition of achievable orderly combinations. That is not a characteristic of the behavior of untrained great apes. Whereas captive apes can unblock tubes to enable drinking, take composite tools apart, and discern some particular physical properties of their constituent parts relevant to obtaining food or drink (such as hollowness or solidity, flexibility, or rigidity; Manrique et al. 2010), they show scant ability to reassemble tools, let alone rearrange their parts in a different self-generated manner that is consistent with some other observable properties (such as shape, color, texture, smell, and so on). Most of their activities with tools seem to be directed at gaining access to food or drink. Arduous training of chimpanzees was needed before two alone among them, even then with much difficulty, began to be able to separate inedible icons representing edible and inedible objects familiar to them, and even others that were unfamiliar, and then to separate their corresponding referential

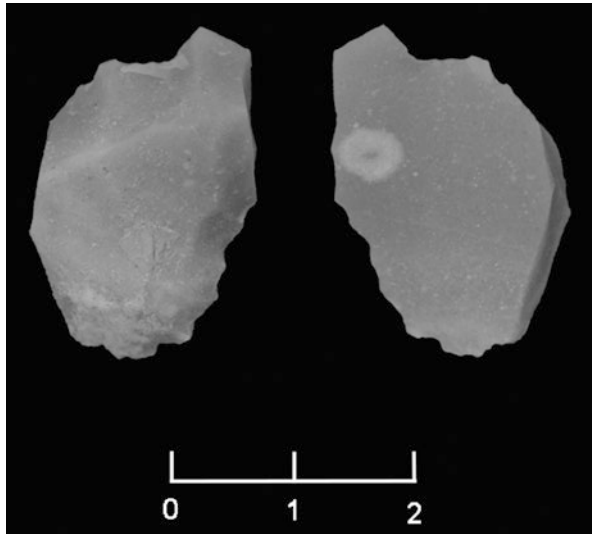


Fig. 4.5 Artifacts from Cueva Negra del Estrecho del Río Quípar, Murcia, Spain (reproduced with the permission of the Murcian Association for the Study of Palaeoanthropology and the Quaternary): knapped discoidal chert core

“lexigram” labels in absence of imagery; their associative learning was contrasted against human semantic comprehension and representational symbolic ability (Savage-Rumbaugh et al. 1980). Great ape behavior does not seem to be influenced by self-generation of alternative referential or indexical ordering that involves both composition and decomposition of often overlapping analogous concepts based on evaluations of similarity and dissimilarity which are important in symbolic thinking (see also Deacon 1997).

Dating from 1.53 Ma (Brown and McDougall 1993), the 1.6 meter-tall *Homo erectus* skeleton (KNM-WT 15000) excavated at Nariokotome in Kenya is that of an 8–9-year-old young person (Dean 2016; Dean and Smith 2009) that was already an adolescent or young adult, comparable in height to modern young adults (Ruff and Walker 1993) and to mature *Homo erectus* specimens elsewhere in Africa after 1.7 Ma (Ruff and Walker 1993). (Some paleoanthropologists prefer to use “*Homo ergaster*” when referring to African *Homo erectus* between 2 and 1.5 Ma.) As in other mammals, its growth was probably determined by growth

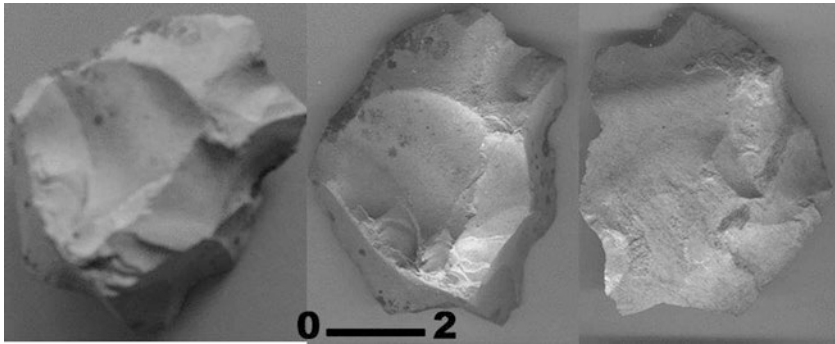


Fig. 4.6 Artifacts from Cueva Negra del Estrecho del Río Quípar, Murcia, Spain (reproduced with the permission of the Murcian Association for the Study of Palaeoanthropology and the Quaternary): knapped discoidal limestone core

hormone. The modern human adolescent growth spurt may not yet have come into existence. The Nariokotome individual may well have had “a late childhood lacking a slowdown in growth,” and, as “an early adolescent at 8 or 9, may have been much more independent than a comparable modern adolescent of 12 or 13 in a traditional society” (Dean and Smith 2009; see also Dean 2016), but with “a lifespan potentially some 15 years longer than a modern chimpanzee” (Dean and Smith 2009), thereby perhaps allowing a few individuals to survive to ≥ 50 years of age, all of which “may throw light on the family structures of early *Homo erectus*” (Dean and Smith 2009). Its 880 cm^3 brain volume is unlikely to have much exceeded about 900 cm^3 even were growth to have continued (Begun and Walker 1993), whereas modern human adult brains have volumes of about 1350 cm^3 (and $1250\text{--}1300 \text{ cm}^3$ had been attained within some Paleolithic skulls by 0.5 Ma). Its coefficient of encephalization is below that of modern humans albeit somewhat high for *Homo erectus* (Begun and Walker 1993). In its brain, myelination of (white matter) neurons, which enhances transmission of impulses, very likely would have been complete before 15–16 years of age, whereas in modern people, it continues until we are about 25 years old.

Today, in the cerebral cortex, white matter plasticity extends beyond childhood and adolescence, particularly after training in particular skills that include some which involve extremely rapid responses to tactile, visual, acoustic, proprioceptive, and kinesthetic inputs, not to mention

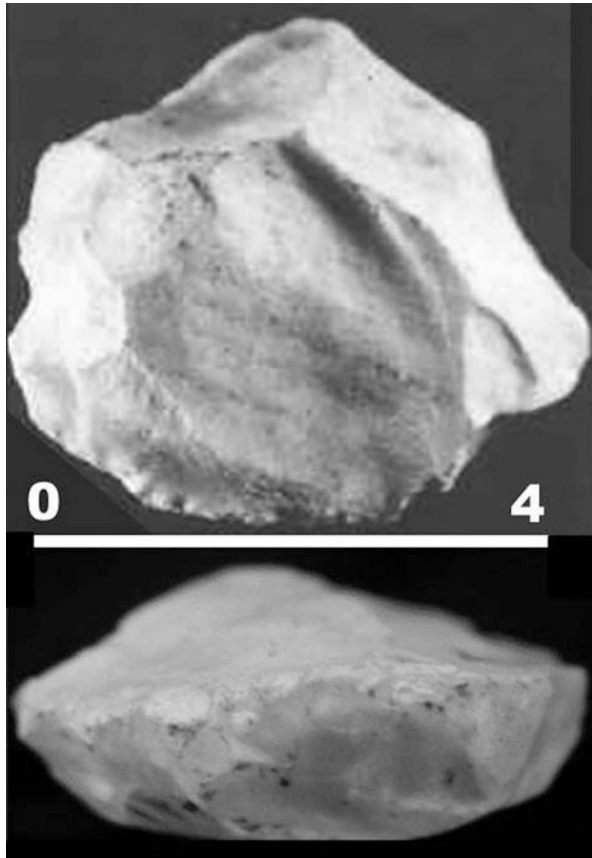


Fig. 4.7 Artifacts from Cueva Negra del Estrecho del Río Quípar, Murcia, Spain (reproduced with the permission of the Murcian Association for the Study of Palaeoanthropology and the Quaternary): knapped discoidal chert core

learnt and remembered information, such as juggling and playing musical instruments (Bengtsson et al. 2005; Roberts et al. 2010; Scholtz et al. 2009). Cognitive enhancement appears to be correlated with the development of microstructural changes in white matter which can be detected by neuroimaging methods such as diffusion tensor imaging (for example, Mandl et al. 2008; Roberts et al. 2010, 2013a). Training also affects white matter microstructure in the cerebellum (Roberts

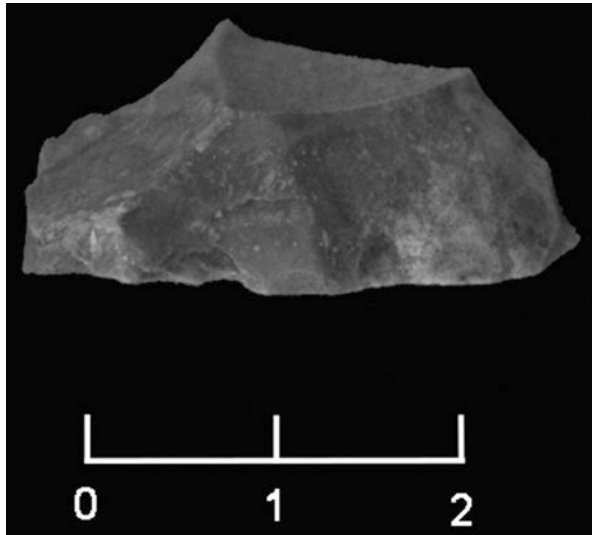


Fig. 4.8 Artifacts from Cueva Negra del Estrecho del Río Quípar, Murcia, Spain (reproduced with the permission of the Murcian Association for the Study of Palaeoanthropology and the Quaternary): knapped discoidal chert core

et al. 2013b) which modulates and refines motor behavior. It has been argued that within anthropoid Primates the cerebellum of great apes and humans seems to have undergone disproportionate evolutionary enlargement, perhaps predisposing toward tool-using skillfulness (Barton and Venditti 2014).

From childhood to adolescence, nowadays, there is an increase in white matter, including in left-sided frontoparietal fiber tracts (Giedd et al. 1999; Paus et al. 1999). Cerebral myelination continues beyond late adolescence (Miller et al. 2012; Sowell et al. 1999). By contrast, in macaques, it is complete by puberty. It may not be altogether complete in pubertal chimpanzees (Sakai et al. 2010, 2011) though it seems to be so a few years later when they have reached full sexual maturity (Miller et al. 2012). The panin and hominin lineages had split around 6 Ma. A plausible conjecture is that cerebral myelination was complete, or almost so, in pubertal hominins around 2 Ma and likewise in the Nariokotome young person of 1.53 Ma.

At the microscopical level, the neuronal anatomy of the anterior part of the prefrontal cortex separates modern human brains from those of all other great apes (Semendeferi et al. 2011); furthermore, the pruning of dendritic synaptic spines in human prefrontal neurons continues after the age of 20 (Petanjek et al. 2011). These are among several aspects that imply an evolutionary trajectory toward a hominin life span characterized by the increasingly protracted growth of individuals (Semendeferi and Hanson 2016). Plausibly, the trajectory involved a gradual process of natural selection, over a long period of Plio-Pleistocene time, in order to establish very many adaptations and achieve their integration such that reproductive success ensued. The relatively greater cerebral expansion in modern children than in young chimpanzees (Sakai et al. 2013) perhaps could be related to increases in brain volume as *Homo* evolved during the Pleistocene.

The communicative skills of the Nariokotome young person may have been little better than those of our 4-year-old children today. Perhaps his mental developmental stage, in terms of the classical Piagetian scheme (Piaget 1977), was one of *preoperational capability* (see also Wynn 1989) and that even the adults around him had scant mental capacity to conceptualize *formal operations* by envisaging abstract considerations about the possibilities of alternative logical procedures or arguments, even were such to have been held in memory or kept in mind (see Piaget 1959). No doubt any such considerations were limited to cause-and-effect sequences involving tangible or visible matters (and maybe even audible or vocal cues or signals), though with some capability of understanding the outcome of making mistakes and how these might be avoided by evaluating the sequences and making adjustments to them by thinking in reverse order so as to make possible the taking of steps in order to minimize mistakes or mishaps. Memory matters greatly if the same mistake is not to be made twice.

It is also likely that there was awareness both that several behavioral sequences were mutually exclusive, and also that, often, backtracking, in order to change from one alternative sequence to another, was precluded by “second-order” recognition of lost opportunities (for instance, When I’m frying an egg I’m aware I’ve lost the opportunity to hard-boil it in its shell!), in so far as some irreversible features of a sequence once embarked upon implied forsaking, once and for all, the affordances of an alternative sequence. Such mutually incompatible sequences may be regarded as

self-constraining. To the extent that, by and large, their different outcomes are determined by sequential behavior, the sequences can be regarded as *self-determining chains of behavior*. From a classical Piagetian standpoint, such recognition of the distinction between reversibility and irreversibility separates *concrete operational* thinking from *preoperational* cognition, and is what renders possible the anticipation of making mistakes and carrying out contingency planning to avoid (or pre-correct) them. Memory is fundamental. A plausible, albeit unfalsifiable, conjecture is that memory skills may have been honed by alloparenting (“grandmother hypothesis”) which could have led to increasing cognitive complexity in response to diverse social interactions requiring the development of abilities to remember different social circumstances (see also Sterelny 2012).

Be that as it may, the part played by memory undoubtedly was important for co-evolution of cerebral and cognitive developments with communal intercourse and behavioral activities with tools, which contributed to singular developments in niche adaptations of late Early Pleistocene *Homo*, dispersed throughout the Old World, surviving and reproducing in environments unlike those of equatorial Africa. Between 1.1 and 0.8 Ma, evidence of fire comes from sites with Paleolithic assemblages containing elongated, bifacially flaked, large cutting tools from caves in South Africa and Spain and an open site in Israel (Alpersen-Afl and Goren-Inbar 2010; Berna et al. 2012; Goren-Inbar et al. 2004; Walker et al. 2016b) and has been claimed at earlier sites in East Africa (for instance, Gowlett et al. 1981). Fire and caves do not characterize the niches of great apes today. Heating foodstuffs derived from animals and plants aids their digestion and absorption (Carmody and Wrangham 2009; Carmody et al. 2011; Wrangham 2009; Wrangham and Carmody 2010). Such foodstuffs, especially fatty acids, underpinned the evolution of *Homo erectus* brains, already twice the volume of the brain of a chimpanzee, plausibly by enhancing neuronal development (Fonseca-Azevedo and Herculano-Houzel 2012). Heating also detoxifies and reduces pathogenic contamination of food (Ragir 2000; Smith et al. 2015). Findings from human molecular genetics suggest that there evolved a growing tendency to conserve energy and reduce demands on it for continual immune upregulation of genes, and imply that adaptation to a cooked diet had taken place before 0.8 Ma (Carmody et al. 2016). The growth of cognitive and behavioral versatility favored reproductive success, dispersal, and adaptability in a wide range of natural environments and ecological habitats in Africa and Eurasia.

The matter now must be considered of the means of transmission of Pleistocene tool-making, tool-uses, care of fire, and other adaptations, in small, fragile, human bands of very young, small-brained, tongue-tied adults (perhaps no more than 50–100 adults and children altogether), exposed to the ever-present likelihood of extinction that assuredly occurred over and over again, thereby extinguishing accumulated memories and opportunities for observational learning from those. Based on neuronal considerations, it has been proposed that making bifacial stone tools co-evolved with incipient “proto”-linguistic ability (Arbib 2011, 2012; see also Aboitiz et al. 2010). The merits of the proposal will be considered further below. However, it is implausible that widespread persistence of a few common types of tools, over thousands of kilometers and hundreds of thousands of years, was maintained by equally widespread persistence of a common linguistic tradition with a constrained vocabulary, which would have had to be narrowly focused in scope while being widely spoken in time and space.

Nevertheless, the archeological record of the Early Pleistocene testifies to developments in hominin cognitive versatility, which were not maladaptive and reflect technical skillfulness requiring manual (haptic) dexterity. Artifacts made by hand involve their makers’ memories of touching and feeling things: haptic memory. Most likely, the observational learning that facilitated transmission of manual skills to others was grounded in their shared biological evolution—of the physiology, biochemistry, and biophysics of cerebral neuronal circuitry—that underpinned and enabled cognitive versatility in human bands that was appropriate for nonverbal observational learning of shared behavioral chains and strengthening thereby of appropriate haptic memories for activities implicit in those chains. The fundamental basis in the evolution of the brain of early *Homo erectus* is more likely to have been at the biophysical neuronal level, affecting memory, imitative behavior, and nonverbal self-generated composition and decomposition of overlapping similar and dissimilar concepts, rather than at a level of using and understanding language which undoubtedly developed from the aforementioned fundamental base (see Wynn 2000). That base will be considered with regard to the complex relationships in the brain between short-term haptic working memory, long-term procedural memory of haptic behavior, and prospective memory. In terms of the three distinct usages of working memory discussed by Beaman (2010), it is used henceforth in the sense of working attention (see Baddeley 2001) which seems to be bound up closely with memory (Cowan 1998, 2005).

First, however, it is convenient to keep in mind that conservatism of behavior following the appearance of *Homo* in the Early Pleistocene likely owes to various factors. Biological lineages and transmission of behavior were exposed to the continual risk of extinction. Unbalanced sex ratios may have hampered reproduction of small groups. Early death was an ever-present risk (especially perhaps from obstructed birth) and skillful knowledgeable elderly adults were few and far between. Compared with Late Pleistocene humans (*Homo neanderthalensis* and *Homo sapiens*), the smaller adult brain of *Homo erectus* at 1.5 Ma contained relatively smaller prefrontal cortical areas for monitoring behavior and integrating active working short-term attentional memory with implicit nondeclarative procedural long-term memory (see below). Cognitive versatility was limited, given that attainment of adult brain size was at about 12 years of age, and myelination of its neuronal axons was probably completed by 15–16, some ten years earlier than today. Communicative skills between adults may have been no more than those of our 4-year-old children. Hippocampal-prefrontal co-activity (see below) would have been low were mature individuals to have faced relatively few demanding tasks and so failed to develop a prospective memory flexible enough for efficient multitasking. The left inferior parietal lobule (see 3.5) involved with tool-use was small, as were prefrontal and parietotemporal areas with mirror neurons, and conservative mirror-neuron circuitry doubtless limited observational learning and hindered imitation of novel behavior (see below). These are all just some of the matters which exerted a strong brake on the rate of technological and “cultural” development during the Pleistocene, and which, if they were not taken into account, might seem to be out of step with the “precocious” appearance by 1.5 Ma of humans similar in height to ourselves.

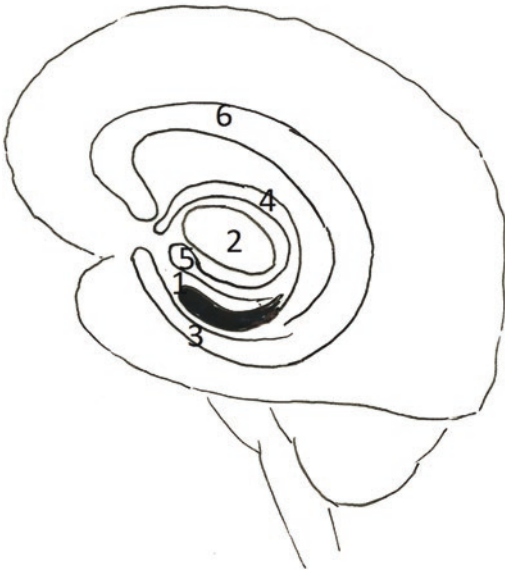
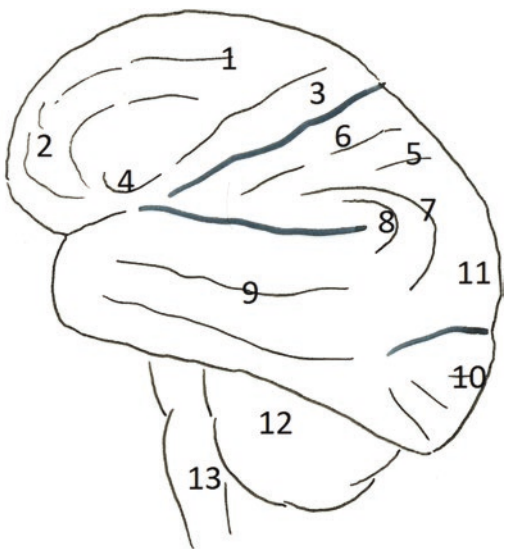
4.3 REMEMBERING TOUCH AND MANIPULATION

Making and using stone tools put demands on how haptic memories of touching and manipulating objects are conserved and retrieved (Walker 2016). Haptic memory involves enhanced intracellular biophysical responses evoked by touch in some cerebral sensory neurons (well demonstrated, from 1970 onward, by neurophysiological experiments on monkeys; Fuster 1999, 2015) with ensuing network effects mediated by prefrontal cortical neurons in functional systems of active working short-term memory by preparing motor neurons to respond instantaneously

(as well as attuning other kinds of sensory neurons), and even to anticipate appropriate responses, implying recourse to acquired memory. It is convenient to call it haptic active working short-term memory (or working attention) in order to distinguish it from active working short-term memory induced by sight, sound, smell, taste, proprioception, and so on (all of these short-term memory modalities involve temporal integration in goal-directed actions and should not be understood as mere precursors of long-term memories; Fuster 2015). In the brain, dorsolateral prefrontal cortex is involved mainly in haptic active working short-term memory (or working attention), though similar effects occur in parietal cortex (Romo and Salinas 2001). Neurophysiological findings show that, compared with visual stimuli, a monkey's attention to tactile stimuli has greater effect in consolidating sensory neuronal responses, an effect that increases with evermore difficult tasks, and intracellular stimulation of sensory neurons can evoke haptic active working short-term memory discriminatory perceptions, such as place order within an ordered series, implying other cells are involved in processing the information (Romo and Salinas 2001; Gold and Shadlen 2007).

Notwithstanding neurophysiological experiments into visual working memory, implicating associative long-term memory in neurons of monkey anteroventral temporal cortex (Miyashita 1988), the need for cognitive constancy when complex goal-directed motor actions are carried out in ad hoc conditions carries wider implications. Important among these is the flexible parallel processing of programs capable of integrating neocortical "motor engrams" (Fuster 1999). Engrams are latent traces underpinning memory (Lashley 1950; see also Semon 1921, 1923), or, more plausibly, neuronal biophysical states (Josselyn et al. 2015; Tonegawa et al. 2015; see below) that can be reinforced by reverberating reentrant neuronal circuits, with cerebellar and subcortical "motor habits ... (that are) ... much more rigid, precise, and of the nature of machine programs" (Fuster 1999, p. 170). Equally important is "classifying and actively selecting motor acts from prior experience (motor memory) that are conducive to their respective goals" (Fuster 1999, p. 169) with regard to rules for performing a task appropriately in time and space, while being protected by inhibitory control from distraction by inappropriate memories or other matters (Fuster 2015).

Fuster's dynamic view of "motor memory" as the synchronous convergence in the prefrontal cortex of programs, available at several different hierarchical levels within the various parts of the brain, eschews



◀ **Fig. 4.9** *Left side of the human brain. Top* an external aspect of cortex; *Bottom:* diagram highlighting some internal neuronal structures. *Top* 1 frontal lobe; 2 prefrontal cortex; 3 precentral motor cortex; 4 areas with mirror neurons and neurons involved in speech; 5 parietal lobe; 6 postcentral somatosensory cortex; 7 intraparietal sulcus; 8 anterior supramarginal gyrus of the inferior parietal lobule; 9 temporal lobe; 10 occipital lobe; 11 parietal precuneus and occipital cuneus areas; 12 cerebellum; and 13 brain stem. *Bottom* 1 hippocampus; 2 thalamus; 3 parahippocampal gyrus; 4 fornix; 5 amygdala; and 6 cingulate gyrus

the notion of a clear-cut separation between short-term and procedural long-term memory (a notion also criticized by Cowan 2005). Indeed, according to Fuster (2001), “Working memory is as widely distributed as the long-term memory that supports it ... working memory is emerging as a mechanism of temporal integration essentially based on the concurrent and recurrent activation of cell assemblies in long-term memory networks of frontal and posterior cortex.” Fuster points out that working memory should not be regarded as being synonymous with short-term memory if the latter is taken to be “the precursor stage of long-term memory” (Fuster 2015, p. 6), and considers that in a “unitary view of memory with a common cortical substrate ... working memory is the temporary activation of *updated* long-term memory networks *for* organizing actions in the near term. That prospective aspect is essential to the definition of working memory” (Fuster 2015, p. 6). This aspect is not confined to the prefrontal cortex.

Lying behind it is the premotor (or supplementary motor) area of the frontal cortex. As well as in both the left middle and inferior frontal gyri, neuronal activity nearby in the left premotor area has been recorded using positron emission tomography when human subjects looked at objects that they *could* but did *not* grasp (Grèzes and Decety 2002), occurring concomitantly with activity in posterior parts of the brain which included the left inferior parietal lobule. Canonical neuronal activity already had been identified in the premotor cortex of monkeys (Rizzolatti and Gentilucci 1988). As Grèzes and Decety (2002) pointed out, such findings have interested researchers concerned with linguistic evolution, on account of the proximity of the inferior part of the left premotor cortex to Broca’s area in the posterior part of the prefrontal cortex, and our capacity for mental “speech” in our innermost silent conversations with ourselves. A plausible conjecture is that recognition

of the affordances of objects of attention, including physical materials for tools and the possibilities of manipulating them, might have played a part in early linguistic evolution (see Arbib 2011, 2012; Arbib and Rizzolatti 1996). There are connections between the premotor cortex and the parietal cortex, particularly the intraparietal sulcus where also there are important canonical and mirror neurons (Rizzolatti and Strick 2013; Rizzolatti and Kalaska 2013; see below) (Fig. 4.9).

Considerations similar to those of Fuster have been offered by other workers; thus, it is “increasingly apparent that it is difficult to frame WM as being supported simply by frontal or frontoparietal brain regions. A substantial body of work now makes it clear that early sensory regions, parts of the basal ganglia and, controversially, even the hippocampus—long considered to be a brain area that is not involved in working memory might play key and differing roles, depending upon task requirements. Some of this work challenges the notion of distinct differences between working memory (WM) and long-term memory (LTM), or at least questions where that division lies” (Fallon et al. 2016; see also, Hartley et al. 2007). Findings from psychophysical experiments, involving neuroimaging and perceptual delay-estimation tasks designed to assess human visual working memory, imply that flexibility of the distribution of shared resources in working memory can order priorities among them with analog processing in stochastic fashion of multiple inputs in parallel (rather than *seriatim*), thereby favoring enhancement of precise short-lived memories (Bays 2015; Bays and Husain 2008; Bays et al. 2011a, b; Gorgoraptis et al. 2011). Findings from these and related experiments suggest that working memory can be regarded as a limited resource characterized by a changing precision of recall, the fidelity of which is influenced continuously by the varying quantities of things to be kept in mind and their differential salience or relevance to a goal (Ma et al. 2014). This modern dynamic approach toward investigating the neural basis of working memory represents a marked departure from widely held considerations defended by many scientists (for instance, Zhang and Luck 2008) about the discrete nature of representations in working memory.

However, the nature of working memory is of concern here only in so far as it impinges on the matter of the differences between great apes and early humans with regard to tool-use and tool-making. A “strong” view of representations held in working memory seems to be implied by the conjecture that “a genetic neural mutation, sometime within the

last 100,000 years, enhanced working memory capacity” (Coolidge and Wynn 2007; see also, Wynn and Coolidge 2004), thereby distinguishing *Homo sapiens* from archaic and earlier forms of the genus (see also, Coolidge and Wynn 2005, 2009; Wynn and Coolidge 2012). This conjecture of an *enhancement* of working memory in *Homo sapiens* owing to a genetically surprising “hopeful monster” is unconvincing from the standpoint of a neo-Darwinian synthesis of the origin of species by a process of natural selection for enduring adaptations that might be understood in terms of population genetics.

Whereas often the Paleolithic archaeology of the past fifty thousand years is invoked as corroborating a notion of acceleration in *Homo sapiens* of cognitive evolution, the unprecedented variety of Late Pleistocene artifacts is explicable, nevertheless, by unsurprising, prosaic biodemographical considerations (Bocquet-Appel and Degioanni 2013; Degioanni et al. 2015). A sufficiently plausible biological conjecture is that evolution of the cerebral neuronal capacity of working memory took place imperceptibly over several hundred millennia, perhaps close to two million years, by adaptive changes mediated by inherited genetic and heritable epigenetic effects which impinged on cognitive abilities and the development of cerebral neuronal capacities for procedural memory, whether we choose to call it long-term working memory or long-term implicit, nondeclarative memory. Considerations of working memory as a limited neuronal resource seem particularly appropriate to envisaging its gradual evolution in *Homo* by imperceptible biophysical and biochemical modification at intraneuronal and synaptic levels.

Psychophysical experiments have shown that parietal cortical sensory neurons stay active for several seconds when a monkey recognizes that an object it touches is the same as one in a photo of two different things it previously had fondled inside a black box. The importance of parietotemporal cortex is acknowledged in intention and definition of manual behavior, related to both prefrontal and hippocampal activity, as well as spatiotemporal ordering (Archambault et al. 2011; Binkofski et al. 1999; Bisley and Goldberg 2010; Bonini et al. 2011; Jenkins and Ranganath 2010; Lee and Rudebeck 2010; Lindner et al. 2010).

Frontal and parietotemporal cortices have expanded greatly since *Homo* first appeared (Bruner 2010a, b; Bruner and Holloway 2010; Holloway et al. 2004; Weaver 2005). Touch and haptic memory of handling things doubtless have played a part and left their handiwork as stone tools in a much longer (3.3 Ma) and far more abundant record

(thus, Stout 2011) than exists for visual memory (≤ 0.1 Ma: ornamentation, decoration) or acoustic memory (≤ 0.01 Ma: language, music) though it is these that tend to dominate discourses in human evolutionary psychology, cognitive evolution, and even neuroscientific research and experimentation, swayed no doubt by considerations of neuroanatomical observations about visual and linguistic–acoustic neocortical cytoarchitecture.

Neuroimaging in humans shows increasingly widespread involvement of different brain regions when knapping (“Oldowan”) chopping tools is replaced by bifacial (“Acheulian”) stone knapping (Stout et al. 2006). Psychophysical experiments with monkeys implicate mirror-neuron circuits in frontal and parietotemporal cortices that can track manual activity they observe being carried out by a handler or even by themselves (Gallese et al. 1996; Iacoboni et al. 2005; Keysers and Fadiga 2008; Nelissen et al. 2011; Rizzolatti and Craighero 2004; Rizzolatti and Sinigaglia 2006, 2008; Rizzolatti et al. 2004). In monkeys, mime fails to evoke the mirror-neuron responses aroused in humans, from which young children’s capability to learn very likely evolved (Oberman and Ramachandran 2007); unlike apes, they appreciate a mimic’s intended action.

One possible model for how mirror-neuron circuits are involved in imitative behavior is as follows (Iacoboni 2005):

1. Visual information is encoded in the superior temporal cortex;
2. The signal is then sent to the posterior parietal cortex which provides somatosensory information about an observed action by means of parietal canonical neurons;
3. The signal is then sent to frontal mirror-neurons to code the goal of the action to be imitated; and
4. However, before a signal is sent to the primary motor cortex, an efferent copy of the motor command is sent back to the superior temporal sulcus in order to match the predicted sensory consequences of a planned imitation to the visual description of the action originally observed: If the match is good, the primary motor cortex initiates the action.

Comparable in several respects to mirror neurons are the “canonical” neurons which are present around the intraparietal sulcus and the superior temporal sulcus. Canonical and mirror neurons differ, because

canonical neurons do not necessarily fire in the brain of an animal while it is carrying out an action (though some may do so). Because mirror neurons exist in the supplementary motor cortex of the frontal lobe as well as in parietal cortex, it is convenient to refer to frontal mirror-neuron circuits and parietal mirror-neuron circuits, or frontoparietal mirror-neuron circuits (Rizzolatti and Sinigaglia 2006, 2008, 2010). Although the widely used term mirror-neuron system was coined by Rizzolatti and Craighero (2004), it is preferable to use the more accurate term of mirror-neuron circuits (Rizzolatti and Sinigaglia 2010).

It should be stressed that mirror-neuron circuits do not store memories, although if they are involved in imitative learning, which is a plausible conjecture, then by matching action observation to action execution, they very well may play a part in the initiation and development of memories elsewhere in the brain. They also may play a part in the development of prospective memory. Neurophysiological research has thrown light on prospective memory and planning (Gilbert 2011; see below) and involves the hippocampus in the medial temporal cortex.

Memories are distributed widely in the brain. They have been evoked by neurosurgical procedures in different regions of the cerebral cortex, when patients even may remark on them explicitly to the operating surgeon. Development and formation of associative memory involve the polymodal area 36 of inferotemporal cortex (probably by cross-modal integration there of haptic, visual, and acoustic inputs) according to psychophysical, neurophysiological, and neuroimaging studies (Miyashita 2004; Osada et al. 2008). The inferior temporal cortex, anatomically close to the hippocampal cortex, handles effortless recall and automatic retrieval of long-term memory, though it probably receives top-down input from prefrontal cortex for active retrieval when an effort is needed to recall something from long-term memory. The cerebellar cortex also can encode memories, especially some that are involved in the efficient or skillful performance of an activity. Widespread cortical areas of the brain handle learnt facts, learnt associations, and learnt performances, to which our attention may be turned with varying degrees of mental difficulty. Forgetting as well as remembering is a daily occurrence. Consolidation of memories and keeping them up to date are necessary for both learning and efficient performance over the long term. The interaction between neuronal networks dispersed within the brain is necessary for paying attention to memories that have been retained of events, things, behavior, or associations between any of these. The memory of things is called

semantic memory. The memory of events is called episodic memory. Together, they are called explicit or declarative memory: We can express them in speech and language. Behavior is more complicated. We can talk about pedaling a bicycle fast or slowly, whereas pedaling is implicit when I say that I rode my bicycle to work. The behavioral memory may be explicit and declarative, or it may be implicit and nondeclarative “procedural” memory. Procedural memory embraces many habitual actions to which we pay scant conscious attention when performing them seamlessly or automatically.

All the aforementioned kinds of memory may be available, or “stored”, in long-term memory. The processes of their initial acquisition and subsequent “storage” for future availability require consideration. First, though, it is worth mentioning that we have other kinds of nondeclarative memories. They include nerve reflexes (for instance, knee-jerk reflex), body pains and states (for instance, headaches, dizziness, thirst, and bowel pains), emotional memories (for instance, anxiety), and conditioned reflexes (for instance, urinating when standing under the shower); it is hard to articulate the particularities of our memories of these succinctly enough to avoid incomprehension or misunderstanding by hearers. Another very important aspect indeed of nondeclarative memory is the preparation, especially in the prefrontal cerebral cortex, of the immediate responses of motor neurons in functional systems of working attention or short-term working memory (Fuster 1999, 2001, 2015). As will be explained below, this is particularly relevant to the rapid manual activity, whether piano playing or stone knapping. For the moment, it is important to keep in mind that memory is distributed widely in cerebral, cerebellar, and subcortical parts of the brain. This applies to explicit and implicit memory. Both work in parallel with the hippocampus and neighboring cerebral structures (entorhinal cortex and limbic system), not to mention others that lie further away. Many different components can be involved when behavior and habits are learnt, whether tacitly or by imitation. The permutations and combinations of neuronal circuits in the brain are many and various. There may even be a sense in which implicit memory supports explicit memory and facilitates the development of cognitive awareness, enhances working memory, and enables long-term working memory.

Paleoanthropologists have dedicated much study to the anatomical expansion over time of the human cerebral (and even cerebellar) lobes, which can be inferred from inspecting the insides of Pliocene and

Pleistocene skulls. Informative as these studies undoubtedly are, they throw no light on the evolution of cerebral structures that lie away from the surface of the brain which is reflected by the inside of a skull. One of these is a relatively small neuronal structure called the hippocampus which is situated in the temporal lobe medially (in other words, toward the middle of the head), and which itself comprises several neuroanatomical parts. Of particular interest are its close neuroanatomical links in the temporal lobe to the parahippocampal gyrus which encompasses the entorhinal cortex. The hippocampus is the subject of authoritative books (for example, Andersen et al. 2007; O'Keefe and Nadel 1978) and thousands of research articles.

The evolution in Primates of the hippocampus, associated cortical and striatal structures, and their complex relations with the cerebellum, sub-cortical structures, and efferent motor systems (see also, Aggleton 2012; Aggleton and Brown 1999; Aggleton et al. 2010; Amaral and Lavenex 2007; Lavenex 2007a, b) perhaps may be regarded as having extended or expanded a primitive navigational capability to encompass far wider ranging, temporal and predictive cognitive encoding or mapping (see Eichenbaum 2004; Eichenbaum and Cohen 2001, 2014). There has been much scientific controversy about possible alternative ways in which explicit episodic or episodic-like memory relate to the learning of behavior, the formation of implicit memory, and the role of hippocampal neurons (for an extensive overview, see Morris 2007). Both in animal experiments and studies on humans, there is a long tradition of research into explicit memory which pays detailed analytical attention, with forensic rigor, to their subjects' familiarity with, or recollection of, discrete and time-limited aspects of things or events. Other research, however, has drawn attention to findings which corroborate inferences that different kinds of relationships between the aforementioned aspects of study might underpin the learning of behavior or the formation of implicit memory, and impinge on neuronal activity in the hippocampus, surrounding structures, and more widely in the brain. This has given rise to concepts such as "configural association" or "conjunctive representation" (Sutherland and Rudy 1989; see also, O'Reilly and Judy 2001), "relational processing," or "relational representations" (Eichenbaum 2004; Eichenbaum and Cohen 2001).

It has been known for decades that hippocampal injuries or lesions interfere with explicit long-term memory in some patients. Mammalian hippocampal neurons play a significant part in spatial awareness and

spatial memory (O’Keefe 2007; O’Keefe and Nadel 1978). It has been conjectured that the human hippocampus might facilitate the recall of (“theory of mind”) information about what other people may know, for which a perspective-taking hippocampal function could have evolved (Murray et al. 2017, p. 375) from a primitive mammalian navigational function (of which aspects persist in human hippocampal function; O’Keefe 2007; Hartley et al. 2007). Nevertheless, “the hippocampus plays a necessary role in ... implicit perceptual learning in addition to explicit memory” (Murray et al. 2017, p. 255). Neuroimaging of human subjects and experimental research support the view that the hippocampus is concerned with facilitation, encoding, and consolidation of “permanent associative links between the pieces of information that define a long-term memory...” (Miller and Cohen 2001).

A long-established view is that the hippocampus plays an important initial part in forming episodic memory about things and events which are then consolidated elsewhere in the brain (Squire and Alvarez 1995; Squire and Zola-Morgan 1991). Furthermore, it has been shown that the hippocampus is involved in pattern recognition (Yassa and Stark 2011); integration of memories, generalization, and inferential transference (Berens and Bird 2017; Schlichtling et al. 2015; Zeithamova et al. 2012a, b); and value-based decision-making (Wimmer and Shohamy 2012), learning and prediction (Pennartz et al. 2011), prospective memory (Gilbert 2011), social cognition (Tavares et al. 2015), and time-dependent maintenance for haptic tasks of motor sequence memories in conjunction with subcortical striatal nuclei (Albouy et al. 2015). No less than the memory of spatial differences, the memory of differences in order or time affects hippocampal neuronal activity. An algorithmic basis for encoding these underpins the concept of “successor representation” (Dayan 1993). Experiments conducted on human subjects find that the concept can help to clarify how abstract knowledge about the associative strength between relationships, including between memories, may be acquired unconsciously in the hippocampal–entorhinal cortex, and lay the ground for implicit learning applicable to goal-directed behavior (Garvert et al. 2017). Presumably, this neuronal capacity has evolved from primordial navigational functions, though only in humans is it possible to detect its ability to effect implicit transference between unconscious memories of discrete matters and indirectly related referents, or even inferred abstract referents, that may be explicitly acknowledged or recalled episodically.

The matter is relevant from the standpoint of the evolution of keeping in mind “what, where, when” (Tulving 1972) and perspective-taking and self-awareness (or “autonoetic consciousness,” thus, Tulving 1983, 2005). They are necessary for undertaking efficient stone knapping, not to mention its apprenticeship. Mastery involves seamlessly blending explicit episodic memories into rapid manual behavior that is being guided otherwise by implicit memory and tacitly learnt responses. It is impossible to know whether the mirror-neuron circuits of nonhuman Primates indicate self-consciousness, and it is unclear to what extent even great apes are capable of mental time travel (see, Suddendorf and Corballis 1997). However, “Not only can humans travel backward and forward in time mentally from the present moment, but they can also contemplate what their cognitions about past and present were or will be at different times in the past or future” (Roberts 2000). The existence of Late Pliocene stone artifacts, and especially those from the Early Upper Pleistocene from about 2 Ma, implies that self-awareness was present in early *Homo*. It may have been present a million years earlier. Knapping a stone artifact combines an automatic skill needing scant attention (like pedaling a bicycle) with awareness of both self-control and the progress of the activity, which relate self to physical context and the hoped-for outcome, as well as the possible future deployment of the artifact.

It goes without saying that storing and updating (re-consolidating) memory, implicit and explicit alike, require continual modulation of synaptogenesis, synaptic strength, and neuronal excitability. There is an extensive neuroscientific literature on these important matters, and readers are referred in particular to the volume on the hippocampus edited by Andersen et al. (2007). Some genetic considerations, however, cannot be passed over here because of their plausible evolutionary relevance.

4.4 ENHANCEMENT OF MEMORY EVOLVED FROM A NEURONAL PROPENSITY IN EARLY *HOMO* BRAINS WHICH FAVORED KEEPING MEMORY UP TO DATE

The many chemical mediators involved in neuronal memory in the brain are under the influence of a myriad of noncoding RNA epigenetic regulators of gene expression, such as long noncoding RNA (lncRNA) and short RNA elements (siRNA, piRNA, and microRNA), which bind either some regulatory proteins (transcription factors) that can enhance

the consolidation of long-term memory in a neuron (such as CREB-1 or cAMP response element binding protein 1) or others (such as CREB-2) that can inhibit it (readers unversed in neuroscience may find it helpful to refer to introductory books, such as Ruby 2008; Squire and Kandel 2003; or to more comprehensive works, such as Andersen et al. 2007; Kandel et al. 2013; Gazzaniga and Mangun 2014).

Transcriptome analysis has facilitated epigenetic characterization of posttranscriptional modification of DNA structure, affecting the chromatin structure of nucleosomes and their constituent histone proteins (for instance, by methylation, phosphorylation, ubiquitination, and acetylation), as well as identification of modifications in kinases, RNA editing, and so on. Intracellular neuronal protein synthesis induced by training is a well-established feature of the development of long-term memory, as numerous animal experiments have shown over the past two decades. It is noteworthy that lifelong neurogenesis occurs in the subcortical striatum and in the medial temporal hippocampal dentate gyrus (Altman 1962, 1963; Altman and Das 1965; Cameron et al. 1993; Inta et al. 2015; Spalding et al. 2013) where it may play a part in both forming (Restivo et al. 2015) and erasing memories (Akers et al. 2014; Frankland et al. 2013).

The importance cannot be understated of the epigenetic effects on the development of individual organisms and their constituent organic systems, including the central nervous system and the brain (Qureshi and Mehler 2014), with even perhaps a transgenerational impact on memory (Bale 2015; Dias and Ressler 2014; Dias et al. 2015), and possible evolutionary consequences in Pleistocene *Homo* (Somel et al. 2013).

Evolutionary consequences of epigenetic effects may well include irregularities in rates of biological change within a lineage of a sexually reproducing species, rates that hitherto have tended to be regarded as invariant. That important possibility could help us to view in a wholly new light the apparent Pleistocene record of nonlinear co-evolution between paleobiological lineages within the genus *Homo* and trajectories of Paleolithic behavior, and lack of parallelism between these in either time or space when viewed in worldwide perspective, so often explained away by the self-serving notion of “homotaxial” change (see Glossary).

Returning briefly to the nuts and bolts of the matter, there have been identified neurons that can encode some engrams (sensu Lashley 1950) in the medial temporal cortical regions of both the hippocampus (dentate gyrus and retrosplenial complex) and the basolateral part of the

amygdala (Josselyn et al. 2015; Tonegawa et al. 2015). Revival of interest in engrams (sensu Lashley 1950) has led to their investigation from the standpoint of the physical or chemical alterations elicited by a stimulus or learning that are necessary for encoding and consolidation in one or various interconnected neurons of components associated with persistence of elements underpinning memory that are able to be reactivated by cues relating to the original stimuli and are open to reconsolidation in updated form. Although often called a latent memory trace, it must be stressed that “an engram is not yet a memory but provides the necessary physical conditions for a memory to emerge” (Josselyn et al. 2015, p. 521).

That consideration, taken together with the aforementioned epigenetic effects, supports a plausible conjecture that some neuronal circuits in brains of early *Homo* had an incipient *propensity* that favored enhancement both of memories by imitative behavior, and also of imagining alternative perspectives by decomposing perceived reality and recomposing chunks that can be envisaged variably, sometimes in apparent contradiction to each other, but which nonetheless can be juxtaposed simultaneously because they represent what *might be* as well as what *is*. This capacity is compatible with concepts both of visual perspective-taking at levels 1 and 2 and also of attribution of false belief (see Sect. 3.6). This ability to blend reality among different potential spheres is yet to be demonstrated experimentally in great apes. An incipient capacity for it is inferred from Paleolithic activity carried out by early *Homo* from 2 to 1.5 Ma (see 3.5; see also Wynn 1989, p. 74). It is plausible that such an incipient capacity underpinned the origins of language (see also, Barnard 2010; Reuland 2010).

Methods involving pharmacogenetics and optogenetics (Goshen 2014) have enabled the characterization of cellular components associated with responses to conditioned stimuli in populations of neurons in the basolateral amygdala and the retrosplenial and dentate gyrus parts of the hippocampal cortex, though because the responses seem to reflect episodic memory much research lies ahead into comparable neuronal analysis of procedural memory for learned motor behavior that might be capable of integrating haptic active working short-term memory into implicit nondeclarative long-term memory. Nevertheless, the aforementioned interactivity between explicit declarative memory and implicit nondeclarative memory in the consolidation of implicit nondeclarative *procedural* long-term memory renders plausible a conjecture that populations of medial temporal neurons may be able to process and update

mnemonic records. If that turns out to be correct, the way will be open to exploring the neuronal mechanisms that underpin the origins of implicit nondeclarative procedural long-term memory in relation to haptic memory and their evolution in Early Pleistocene *Homo* after 2 Ma.

4.5 IMPLICIT PROCEDURAL LONG-TERM MEMORY, HAPTIC MEMORY, AND PLIO-PLEISTOCENE STONE ARTIFACTS

Chimpanzee brains differ from ours. Unlike chimps, we have a well-developed inferior parietal lobule, which is significant here (the memory neuron circuits are involved also in our left-sided prefrontal Broca's cap area that chimpanzees lack). The anterior supramarginal gyrus of our left inferior parietal lobule in humans is involved when we humans use tools (Peeters et al. 2009). "It is, therefore, conceivable that it houses neurons with mirror-neuron-like properties (Rizzolatti and Craighero 2004) that allow for both tool use and tool-use understanding. This may support tool imitation and learning by imitation. A word of caution is of course needed, as the presence of mirror neurons has yet to be demonstrated in the anterior supramarginal gyrus (aSMG), and their presence is a necessary but not sufficient condition for imitation to develop" (Orban and Rizzolatti 2012, p. 234).

A brief digression is relevant. After training, simple tools are assimilated into the nonvisual topographically organized neuronal representation of macaque brains, with anatomical extension of output axons of some temporoparietal neurons into superficial layers of the intraparietal sulcus, where there are canonical neurons and where they can make contact with parietal neurons (Iriki 2006; Iriki and Sakura 2008), though assimilation of a tool into representation of their hands ceases when the tool is not being used as such. Plausibly, parietal expansion during human evolution was enhanced by natural selection once hominins began using tools regularly. The experimental findings indicate the complex multimodality or polymodality, as well as the plasticity, of intracortical neuronal circuits developed through learning. The polymodality integrates what a monkey keeps in its field of vision with its spatiotemporal actions, and in particular, there appear to be ordered neuronal circuits underpinning the integration between the parts of its visual field, which are receiving attention and the corresponding movements of parts of the body with appropriate timing and orientation (Maravita and Iriki 2004;

Maravita et al. 2003). Alternative responses are thereby *anticipated*, *adopted*, and *adapted*, with *immediacy* nay, almost *instantaneously*. However, transcranial magnetic stimulation (TMS) findings in humans show that the ventral premotor frontal cortex and its connections with the anterior intraparietal sulcus play a part when our fingers prepare to grasp objects with precision, and our grip, moreover, is affected unconsciously by words or numbers we hear or see, implying prefrontally derived cognitive modification of responses of muscles and joints as they undergo transformation in response to posterior visuo-spatiotemporal inputs (Olivier et al. 2007); TMS findings show that our perception of touch in parietal cortex is enhanced by visual stimuli (Ro et al. 2004). If monkeys' brain cells respond in basic ways that are doubtless present in great apes and humans, then what makes *us* different? It seems unlikely that, in preparing monkeys and apes for experimental replication of cortical neuronal working-memory acquisition, the task-discrimination training, through which a human researcher puts the animals, represents a difference from their everyday behavior in the wild that goes beyond one of mere degree. After all, leaving aside the well-studied capabilities of great apes, even "lowly" monkeys have been seen to copy behavior from one another, such as washing sweet potatoes before eating them, or even banging one stone on another.

Intentionality apart, what is the relationship between haptic memory and the mirror-neuron circuitry that registers manual activity, and what might we learn about how active working short-term memory relates to implicit long-term memory? Cerebral recursion, error-detection, and error-correction were prerequisites for both early stone knapping and protolanguage (see also, Arbib 2011; Rizzolatti and Arbib 1998; Stout et al. 2008), notwithstanding innate mirror-neuron conservatism (demonstrated by neuroimaging) that doubtless was a protective outcome of natural selection and maintained a brake on cognitive evolution in Pleistocene *Homo* (see also Calvo-Merino 2005). Implicit long-term memory involves childhood development of preferential neuronal coding and circuitry linking frontal cortex and parietotemporal cortex to the subcortical dorsolateral striatum (caudate nucleus, putamen) and hippocampal cortex (Ashby et al. 2010; Doyon and Benali 2005; Pennartz et al. 2011), and throughout the limbic system, basal ganglia, and cerebellum (Balsters and Ramnani 2011; Balsters et al. 2013). While a discussion of linguistic origins is beyond the scope of this book, a plausible theory of the evolution of working memory implies their appearance in

early *Homo* (Barnard 2010), and also, it has been argued from cognitive linguistics that a necessary preliminary must have been a recursive capability of working memory that enabled a declarative-procedural interface (Reuland 2010); both considerations are relevant to the matter of envisaging representations of not only what *is* but also of what *will be* or what *could be* or *might be*.

Of particular interest for implicit nondeclarative procedural long-term memory storage are neocortical–basal ganglia feedback loops (both negative and positive) between neocortical areas and subcortical striatal subregions, with downstream projection to habenula, pallidum, globus pallidus, ventral tegmental area, and substantia nigra, linked to thalamic nuclei projecting back to the neocortical areas of origin (Hazy et al. 2007; Kreitzer and Malenka 2008). This complexity is why implicit long-term memory is much harder to investigate by functional connectivity analysis than are short-term active working memory or even declarative episodic and semantic explicit long-term memory. Whereas frontal, parietotemporal, and cerebellar cortices may leave paleoneurological endocranial signatures in hominin skulls, medial cortical structures leave none.

The particularly abundant interoceptive Von Economo spindle cells of our (extrahippocampal) anterior cingulate cortex and insula (de Sousa et al. 2009) may be a Pleistocene outcome of increasing self-generated inputs to long-term memory (see, Allman et al. 2005; Petersen and Posner 2012) facilitating “the unique capacity for the intergenerational transfer of the food and information characteristic of human extended families” (Allman et al. 2002), with the particularly large human insula affording “a potential neural basis for enhancement of social cognition in association with increased brain size” (Bauernfeind et al. 2013, p. 269).

The medial frontal and anterior cingulate cortical relationship is undoubtedly important in monitoring and evaluating the behavior of oneself and others, and in detecting errors, especially when a task in hand is changing (Rushworth et al. 2007; Neubert et al. 2014). Human posterior cingulate relationships also are important: Our inferior parietal lobule embraces the supramarginal gyrus, angular gyrus, and parietotemporal junction, and functional imaging shows this region to be involved with keeping close attention to matters not only visuospatial (as in the macaque’s homologous area 7a) but also to unexpected salient aspects regardless of whether sight, touch, or hearing are involved (Husain and Nachev 2006; Nachev et al. 2008).

This cross-modal or polymodal ability of the large human inferior parietal lobule may well have been facilitated by its occupying a relatively more dorsal position in the parietal cortex than that of the extrastriatal motion-sensitive (V5/MT) area of monkeys (relatively closer to their superior parietal lobule and anterodorsal cortex beyond), which may lead to their visuospatial inputs often predominating over those of other sensory modalities. In any event, there is little doubt that inferior parietal lobule expansion had important consequences for the evolving human brain (so also, of course, did relative expansion of white matter, and myelination continuing into and beyond our adolescent growth spurt). The precise genetic mechanisms underlying human cerebral evolution are unknown but may involve *ASPM* and *MCPH1* genes (Gilbert et al. 2005; Konopka and Gerschwind 2010).

Getting back to touch, when blindfolded right-handed people undertake variably delayed match-to-sample tasks, with their right hand rotating an object such that it is either a mirror image of, or parallel to, one rotated by the left hand, functional imaging detects early activity in anterior prefrontal cortex followed by left parieto-occipital cortical activity (Kaas et al. 2007). An early sensory stage of haptic active working short-term memory involves the primary somatosensory cortex in prefrontal cortex, and early in the delay period, initial haptic sensory traces maintained in the contralateral (left) sensorimotor cortex are transformed into haptic spatial representations, maintenance of which engages anterior prefrontal and parieto-occipital cortices. The right-handed response involves activation of other left cerebral regions (superior and inferior temporal cortex, superior parietal lobule, superior occipital cortex, and precuneus), right cerebral regions (insula, superior temporal gyrus, post-central gyrus, and inferior parietal lobule), and also bilateral activity (in the cuneus and parieto-occipital sulcus).

On increasing the delay period from 0.5 to 5 seconds, activity is seen in left anterior prefrontal and parieto-occipital regions and right primary motor, in frontal and occipital cortices. On further increase of the delay period to 10 seconds, left-sided cerebral activity occurs in the rostral part of the occipital, parieto-occipital, and anterior prefrontal cortices and the putamen, bilateral activity in the occipital cortex and right-sided activity in the right anterior cingulate cortex. “The involvement of occipital and parieto-occipital regions in exploration and matching is consistent with subjective reports of visual imagery from the majority of ... participants

and the important roles of (higher order) visual areas for spatial processing” (Kaas et al. 2007); this is in line with electrophysiological findings in monkeys of the cross-modal involvement of the occipital visual cortex during haptic experiments (Zhou et al. 2007). In short, haptic active working short-term memory for touch involves dynamic spatiotemporal neuronal networks of increasing complexity: “associative aspects of a haptic WM task are distributed in a wide network of neurons in motor and parietal areas” (Zhou et al. 2007). Other neuroimaging studies (for example, Meyer et al. 2011) draw attention to cross-modal sensory processing, reaffirming earlier proposals by Fuster (1999).

The matter has great relevance for functional imaging findings during stone knapping. Plausibly, accurately repeated preparation of effective stone tools went hand in hand, so to speak, with preferential natural selection for those cerebral networks for appropriate active working short-term memory. Neuroimaging during stone knapping implicates ongoing monitoring in the superior parietal region of work in hand, involving “dynamic coupling between multiple modes of sensory perception and motor action. Its heightened activation during ‘Oldowan-style’ stone knapping of chopping tools clearly reflects on the complexity and elaboration of the polymodal mappings involved in the perception-through-action of knapping-related affordances” (Stout 2005; see also, Stout 2006).

The approach was extended to include “Acheulian” bifacial stone knapping. Of particular interest were the findings that strong inferior parietal lobule activation occurred bilaterally during “Oldowan” tool-making, and that during Acheulian hand-axe preparation, there was noteworthy activation of the right frontal lobe, both in the ventral premotor area and prefrontal cortex, which underlines the importance of the right hemisphere in controlling the left hand to change the position of a stone, held in it, being knapped by the right hand controlled by the left hemisphere. Ventrolateral prefrontal cortical activation during “Acheulian” tool-making reflected “cognitive demands for the coordination of ongoing, hierarchically organized action sequences” and implied “monitoring and manipulation within working memory” (Stout et al. 2008). Did absence of activation in dorsolateral prefrontal and anterior cingulate cortices mean little advance planning was involved? Not necessarily, because neuroimaging of subjects, who were performing tasks involving varying degrees of complexity of both active working short-term memory and spatial processing, revealed a significant interactive

effect on right posterior hippocampal and bilateral parahippocampal activity, with increasing spatial complexity of the task, which was not found by increasing the demand on working memory, and it was suggested that those cerebral areas “may play a critical role in processing complex spatial representations, which, in turn, may form the basis of short- and long-term mnemonic processes” (Lee and Rudebeck 2010). Finely tuned behavioral timing is associated also with parahippocampal and hippocampal activity and may play a part in implicit long-term memory (Hsieh et al. 2014; Jenkins and Ranganath 2010).

An intriguing comparison (Stout et al. 2015) of functional connectivity, over a period of time during which “Oldowan” and “Acheulian” stone knapping techniques were being learnt, shows interesting differences between these with regard to left superior frontal gyrus activity. An aim of the study was to investigate possible distinctions in knappers’ judgments concerning the physical accuracy of predicted outcomes as against their strategic appropriateness in making the desired tool. It was suggested that such distinctions could be relevant to interpreting subtle differences involving procedural-memory-*versus*-declarative-memory (*savoir faire*; “know-how”) and perceptual-motor-*versus*-cognitive-skill (*connaissance*; “knowledge about”). Occipital cortical activity responded to changing visual attention, and fluctuating parietal activity in the right intraparietal sulcus and precentral gyrus may reflect practice. Whereas left superior frontal gyrus activity in response to the “Oldowan” knapping strategy decreased over time, it stayed constant in response to predicted “Oldowan” outcomes. A different pattern was observed of low, constant response to the “Acheulian” strategy throughout the learning period, which was accompanied by a decrease in response to predicted “Acheulian” outcomes.

The differences imply that the students were trying out *different* cognitive strategies *differently* while they were learning. Separate parts of the left superior frontal gyrus seem to be related in coupling or feedback circuits for somatomotor “control” or “default,” involving the anterior and mid-cingulate cortex, right middle frontal gyrus, inferior frontal gyrus, precentral gyrus and operculum, visual cortex, and cerebellum. Probabilistic functional connectivity analysis supports several of these relationships, and, most significantly in the case of “Acheulian” knapping, the involvement of the right middle temporal gyrus. The study has implications about the interplay between the cerebral processes that underpin how conceptions of alternative strategies and desired outcomes

impinge variably on the development of haptic procedures, and probably the enhancement of their incorporation into implicit memory. A plausible conjecture is that levels 1 and 2 perspective-taking (see above) evolved hand in glove with the development of the aforementioned neurophysiological aspects when some australopithecines evolved into the genus *Homo* that thereby and thereafter diverged behaviorally from all other hominid taxa in a fundamental way.

Early *Homo* survived, so to speak, on a knife-edge, or at any rate on the knapped edge of a stone artifact. Subsequent evolution was touch-and-go, both figuratively and from a standpoint of haptic cognition!

4.6 EARLY STONE-ARTIFACT FORMS, BEHAVIOR, AND PERSPECTIVE-TAKING

The foregoing considerations should caution us against imagining that in the Late Pliocene and Early Pleistocene, there was observational learning by hominins and behavioral transmission thereby. More likely, individual behavior involving modification of stone took place sporadically, enabled by infinitesimally slow changes in propensities of neural networks, which nevertheless could be favored by natural selection during hundreds of thousands of years.

A cognitive matter of some interest in Paleolithic studies concerns the relationship between recognition of different volumes implied by non-secant, symmetrical secant, and asymmetrical secant forms that can be knapped (White and Pettitt 1995), and alternative repeatable knapping strategies, capable of producing alternative outcomes repeatedly. A well-known early Paleolithic strategy was the flaking or fashioning of elongated large stones to make “Acheulian” bifacial artifacts (hand-axes and cleavers) with a more or less symmetrical secant plane (think of slicing a pear lengthwise into equal halves). Their widespread presence by 1.2 Ma implies that spatial concepts of three-dimensional symmetry reflected an “internal reference frame” in *Homo erectus* whereby the “whole tool ... had to be conceived ahead of time” (Wynn 1989, pp. 63–64). An understanding of perspective enabled knappers to “step away from the tyranny imposed by direct perception and construct alternative views,” which “requires the subjugation of what one actually sees to what one thinks” (Wynn 1989, p. 64).

Yet another aspect of that was the appearance around 1.3 Ma (de la Torre et al. 2003) of so-called *débitage* knapping, which involved

“Levalloisian” preparation of stone cores (often roundish, sometimes oblong) with an asymmetrical secant plane (think of slicing a cupcake horizontally into unequal upper and lower portions) that enabled removal of oval, triangular, or oblong flakes (leaving behind a corresponding negative scar, often on a small biscuit-size core that cannot be reduced further). It is plausible that stone tools resulting from “Acheulian” and “Levalloisian” reduction sequences reflect the limited mechanical outcomes that are possible from sequential or recurrent psychomotor and neuromuscular interactions between visuotactile and manual responses to the clues left on a core undergoing rotation during knapping (see also Van Peer 1992, pp. 35–54). (The matter is rather more complicated because some hand-axes have twisted profiles [Roe 1968] and others have broken, incomplete, or partial symmetry; Wynn 2002; see also Abramiuk 2012, pp. 188–192.) Evidence of the two aforementioned knapping strategies present before 1 Ma supports an inference that *Homo erectus* already had “ability to perform action *in thought*” (Wynn 1989, p. 74), and sometimes to have had mental representation of alternative sequences of behavior, albeit perhaps still preoperational in Piagetian terms (see Wynn 1989, 74).

The useful formal distinction enshrined in archaeological notions of “*façonnage*” or fashioning, and “*débitage*” or extracted flakes (Boëda et al. 1990), may be an oversimplification (see also Stout 2011), but it can be helpful from a cognitive viewpoint, especially if combined with concepts of symmetry and asymmetry (see, for example, Wynn 1989; Wynn and Coolidge 2010), though the methodology of analytical inspection of lithic reduction sequences (or *chaînes opératoires*) on which the notions are based is open to criticism on the ground of undue subjectivity of interpretation (McPherron 2013). Fashioning an almond-shaped biface out of a flat almond-shaped stone may allow the knapper to keep in sight an ostensive relationship between the shape of the stone and that of an intended flaked biface. The same applies, in part, when long slivers or blades are struck from a prepared prismatic core, as if staves were being removed from the surface of a barrel, so to speak; this technique became widespread in some parts of the world after about 0.035 Ma (35,000 years ago).

Very different, however, is the situation the Levalloisian knapper confronts. Here, the desired final flake (or *éclat préférentiel*) to be extracted lies, as it were, hidden from view, less foreseeable than the yolk inside a hen’s egg or the creamy center of a cupcake, and unimaginable simply

from looking at the external shape of the stone before the Levalloisian core-reduction sequence begins. “Early stone-knapping techniques like Levallois ... and early stone tool types such as twisted profile handaxes ... require a complexity of images held in... working memory ... No more complex form of stone knapping *ever* appears” (Coolidge and Wynn 2005, their emphasis). From one particular refitted Levalloisian knapping sequence at a Dutch Middle Pleistocene site, the existence was inferred of an underlying “plan-like principle” that likely had set out a practical objective while letting the knapper monitor the work in hand so as to allow transformation in a fluid yet structured “configuration of possibilities” (Schlanger 1996).

Again, where hand-axes are symmetrical, then “spatiotemporal substitution and symmetry operations” were required that are more complex, cognitively speaking, than are “the spatial concepts necessary to manufacture blades” removed from a prepared pyramidal core (Wynn 1979, p. 385), because making hand-axes involves envisaging shapes and volumes from alternative perspectives, rotated in the mind, while paying attention to three-dimensional congruent symmetry. This characterizes several very elegant Middle Pleistocene hand-axes, manifesting “essentially modern intelligence” (Wynn 1989, p. 92). Hand-axes have been interpreted as exemplifying evolution of diffuse “constellations of knowledge” (Wynn 1995, p. 18; see also Wynn 1989, 1993) that favor behavioral plans of action involving feature correspondence as well as the complex cognitive skill of reversibility, which, nevertheless, could well have been learned and communicated by simply observing and copying. As Wynn (1995, p. 21) put it: “it would be difficult to overemphasize just how strange the handaxe is ... it does not fit easily into our understanding of what tools are, and its makers do not fit easily into our understanding of what humans are.”

Serious criticism, based on reasonable epistemological grounds, has been leveled (de la Torre and Mora 2009) at dialectical cognitive inferences drawn from formal geometrical considerations of Paleolithic flaked artifacts. The matter is certainly important but perhaps it can be sidestepped with advantage by adoption of a modal approach to stone knapping favored by Shea (2013, 2016), which embraces a range of flexible cognitive relationships between knappers and lithic affordances, and avoids preconceived notions about how behavior may have undergone change. This is, without doubt, an area in which research is ongoing. The interest of one of us (MJW) was stimulated by identification

of different procedures of stone reduction at a 0.8 Ma site in southern Spain (Cueva Negra del Estrecho del Río Quípar in Murcia province) which imply that choice was exercised by those who frequented it (Walker 2009; Walker et al. 2013, 2016a, b). They imply evolved enhancement of long-term implicit (nondeclarative) procedural haptic memory. Moreover, they imply recognition of irreversibility, once embarked upon, of each of the respective behavioral chains of activity. From a Piagetian standpoint (see Piaget 1977), presence at one site of alternative chains of knapping behavior reflects early evolutionary appearance in *Homo* of *concrete operational* thinking, in so far as representational ability to envisage reversibility or its impossibility (owing to incongruity with an internal frame of reference) is conspicuous by its absence in preoperational cognition.

4.7 PROSPECTIVE MEMORY

Of interest from the viewpoint of behavioral modification is the demonstration (by functional connectivity analysis of magnetic resonance imaging) that distracting someone's attention away from his prospective memory concerning an intended behavior, and toward some other matter, allows, nevertheless, the former intention to be kept in medial temporal cortex. Here, there is noteworthy bilateral hippocampal activity whenever activity in the rostrolateral prefrontal cortices is correlated with postponement of the execution of the former intention, and also involved are the insulas and anterior cingulate cortices (Gilbert 2011). The neurobiological implication for apprenticeship is clear. Moreover, it appears that "the hippocampus and prefrontal cortex are coactive in early adolescence regardless of task demands or performance, in contrast to the pattern seen in late adolescents and adults, when these regions are coactive only under high task demands ... neural circuitry underlying working memory changes during adolescent development" (Finn et al. 2010); albeit a minority view, some psychologists argue that a notion of "long-term working memory" need not be a contradiction in terms and could account for development in some people of singular skills or aptitudes (Ericsson and Delaney 1999; Ericsson and Kintsch 1995; Ericsson et al. 2007). Some observations on great apes are possibly compatible with a similar interpretation (Manrique and Call 2015). If early *Homo erectus* did not undergo fully the adolescent growth spurt as we know it, then it is likely that integration of its hippocampal–prefrontal activity was

underdeveloped compared to ours and was less able to retain prospective memory and engage in multitasking.

Because prospective memory involves recall, it is a hard task to disentangle the relationship in the brain between episodic and habitual referents of prospective memory, that is to say, between its event-related and time-related contents, which over time seem to change inversely on habitual repetition of a task where close attention can be relaxed. Neuroimaging and EEG-ERP studies on humans find that occipital cortex is involved, including particularly the cuneus, the precuneus of the parietal cortex, and the inferior parietal lobule, as well as the superior temporal gyrus, cerebellum, anterior cingulate, and dorsolateral prefrontal cortices, especially right prefrontal cortex, where activity decreases over time when the content of prospective memory is time-related and where lesions impair prospective memory (Burgess et al. 2001, 2011; Gonneaud et al. 2014; Volle et al. 2011; West 2011). Anatomical evolution of the modern human parietal precuneus might correspond to significant developments in human cognition with respect to archaic humans, such as Neandertals (Bruner and Iriki 2016; Bruner et al. 2016), and its close relationship with the posterior cingulate gyrus and retrosplenial cortex is doubtless relevant (Bruner et al. 2014). Whereas the paleoneurological signature of the precuneus may well be reflected in craniometrical evolutionary changes in the parietal bone, deep connection with the posterior cingulate gyrus reminds us that, once again, cerebral areas are also involved that lie medially and therefore leave no paleoneurological signature.

Only recently, relationships have been determined between time-based aspects of human prospective memory and cerebral areas. It is difficult to design psychophysical experiments to investigate them in apes or monkeys. Holding things in mind, while diverting attention to others, is a remarkable aspect of human attention and planning. Rather than the craniological record, plausibly, it is the Paleolithic record that affords us the best testimony to the evolutionary enhancement of implicit nondeclarative long-term procedural memory and of the effective prospective memory that allowed some things to be kept in mind while other things were being held in the hand and subjected to complex haptic operations. Memory matters.

When haptic (or other) procedural or habitual tasks that demand attention are interrupted, we often can retain them in prospective memory and soon return to them, or even alternate between them seamlessly (multitasking). No doubt this was very hard indeed for Early Pleistocene

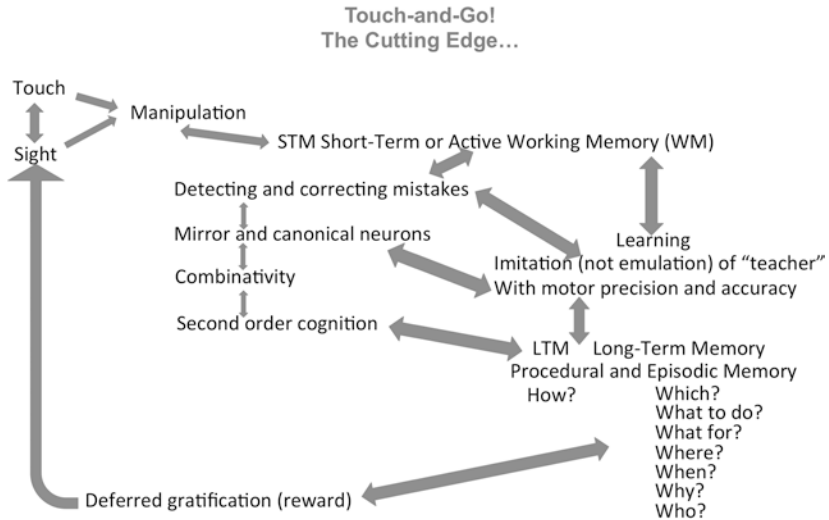


Fig. 4.10 Touch-and-Go! The cutting edge: Memory was fundamental

Homo erectus brains in which fairly rigid neuronal circuits were established early in life. Our prospective memory is an evolutionary outcome from two million years of integrating active working short-term attention with implicit procedural long-term memory (Fig. 4.10).

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Concluding Remarks

Abstract Great ape behavior with tools is significantly different from that of humans, including that of early *Homo* between 2 and 1.5 Ma. Whereas great apes are skilled with tools, can identify their functional properties in relation to a task in hand, and are capable of solving some problems, they nevertheless lack that capacity for foresight which enables flexible representation of possibilities that might be envisaged albeit not seen hitherto. This cognitive limitation underlies their inability both to assemble multicomponent tools and to manage false-belief attribution. The evolution of memory in the brains of early *Homo*, implied by the diversity of stone artifacts after 1.7 Ma, laid the foundation for human cognitive versatility.

Keywords Evolution · Early Pleistocene · Human brain · Cognitive capacity · Paleolithic · “Blending reality among different spheres”
Imagination

Abbreviations

“Ma” = million years ago; Ma is an official scientific abbreviation
designated by the International Union of Geological Sciences
“et al.” = and others, and colleagues
“etc.” = and so on

“p.” = page
 “pp.” = pages

5.1 TEXT

From the standpoint of inquiry into the evolution of human brains and their cognitive capacity, significant theoretical consequences can be inferred from drawing comparisons and contrasts between technical competence in great apes today and its manifestation in the Paleolithic handiwork of Late Pliocene australopithecines and Early Pleistocene humans. It is not enough to point to the superficial likeness between some objects used as tools by great apes and others that used to be made by humans (or may be used still by some of us today). Apparent similarity and analogical appeals to it can be misleading; analogy does not imply equivalence, let alone identity. Instead, detailed attention must be paid to those cognitive aspects of using or making tools which can be related to empirical inquiry grounded both in the critical scrutiny of controlled experiments into the behavior of apes with objects, and also in contemporary research into the functioning neuronal circuitry of human and Primate brains in relation to handling tools. It should be borne in mind that preparation of a stone tool requires both a cognitive ability to recognize what functional properties it should have in order to be suitable for those tasks in which it likely will be used, and also cognitive capacities for short-term, long-term and prospective memory, self-control, planning, ordering behavior, and decomposing reality by separating aspects of it into appropriate representations for guiding the work in hand.

Great apes can detect some properties a tool must have in order to be suitable for solving a given problem (Manrique et al. 2010; Manrique and Call 2011). Their capacity for self-control may approach that required to make a stone tool because although deferral of gratification by apes usually lasts barely 15 minutes (Beran et al. 1999; Beran and Evans 2006) sometimes it may extend to 70 minutes (Osvath and Osvath 2008). Some great apes have shown a capacity for self-control sufficient for that needed to make a stone tool. Chimpanzees have shown an ability to remember where materials suitable for making a tool were left before recovering them 14 hours later (Mulcahy and Call 2006). Their capacity for prospective memory is unclear, however, given that studies admit alternative interpretations (Dufour and Sterck 2008; Martin-Ordás et al. 2010; Osvath and Osvath 2008; Osvath and Persson 2013; Suddendorf et al. 2009). Conspicuous by its absence is

experimental evidence for any ability of great apes to blend reality among different potential spheres. This is fundamental when knapping a stone tool because usually an active representation of a desired outcome will be kept in mind and continually contrasted against the ongoing work in hand (whether the intended product, an unintended accidental “mistake,” or merely a “waste” by-product of knapping). Such representation reflects our capacity to decompose knowledge about reality into chunks available for self-generated imaginary alternative compositions which, apparent contradictions notwithstanding, can be juxtaposed simultaneously nevertheless, because they represent what *might be* as well as what *is*. This capacity is compatible with concepts both of visual perspective-taking at levels 1 and 2 and also of attribution of false belief. There are opposing interpretations of visual perspective-taking: Whereas Tomasello and his colleagues attribute mentalistic capacities to apes, Povinelli rejects that view. Several findings of level 1 visual perspective-taking seem to support the former position, though it is unclear that a supposedly definitive experiment (Karg et al. 2015) provides conclusive support for level 1 capacity of chimpanzees, and their capacity at level 2 is less clear still (Karg et al. 2016). As for the attribution of beliefs, the failure of many endeavors to demonstrate evidence for it in chimpanzees (Call and Tomasello 1999; Kaminsky et al. 2008; Krachun et al. 2010) exceeds descriptions of positive findings (O’Connell and Dunbar 2003; Krupenye et al. 2016).

For those practical manual behaviors involved in knapping stone tools, the capacity for perspective-taking depends on seamless integration of haptic short-term working (attentional) memory with long-term memory (implicit nondeclarative and procedural, as well as explicit declarative and episodic). Early integration can be inferred from bifacially flaked Paleolithic tools made by *Homo* by 1.7 Ma. An incipient propensity of cerebral neurons, favoring both the requisite enhancement of memories of imitative behavior and also the capacity to imagine alternative perspectives, is compatible with modern considerations, both of the “necessary physical conditions for a memory to emerge” (Josselyn et al. 2015, p. 521) in neurons in the brain (see also, Tonegawa et al. 2015), and also of epigenetic impingement on neurons of the central nervous system and its evolution (Bale 2015; Dias and Ressler 2014; Dias et al. 2015; Qureshi and Mehler 2014; Somel et al. 2013). When humans use tools, neuroimaging highlights the singular part played by the anterior supramarginal gyrus of the left inferior parietal lobule (Peeters et al. 2009)

and, given that the lobule lies close to mirror-neuron circuits in the intraparietal sulcus which are active during imitative behavior, a plausible conjecture (Rizzolatti and Craighero 2004) is that those parts of the parietal lobe are involved with how we *understand* tools as well as how to use and make them, assuredly referring our behavior to that of other individuals from whom we can learn by imitation. Probably, tool-use and preparation played a part in natural selection for cerebral expansion in *Homo*. The neuronal substrate is well developed in humans with large brains, though its evolution surely included prior stages of development in early humans with small brains, clear testimony to which is afforded by bifacially flaked stone artifacts from 1.7 Ma when early *Homo erectus/ergaster* made “Acheulian” hand-axes and cleavers in Africa. Less can be inferred from earlier (“Oldowan”) flaked stone artifacts, though neuro-imaging studies (Stout et al. 2008, 2015) suggest that knapping them makes fewer cognitive demands and, interestingly, that *different* cognitive strategies may be involved *differently* during the respective processes of learning how to knap bifacial “Acheulian” artifacts in contrast to “Oldowan” ones.

Several regions of the brain are active when we make tools. Mirror-neuron circuits are important in prefrontal cortex where haptic active working short-term (attentional) memory first was demonstrated in monkeys by intracellular neurophysiological research (Fuster 1999, 2015, and references contained therein) though regarded as interrelated with long-term procedural memory and reinforced by reverberating reentrant neuronal circuits, with cerebellar and subcortical “motor habits ... (that have) ... the nature of machine programs” (Fuster 1999, p. 170). Fuster (2001) regards working memory as being “as widely distributed as the long-term memory that supports it” and “based on the concurrent and recurrent activation of cell-assemblies in long-term memory networks of frontal and posterior cortex.” Unsurprisingly, haptic active working short-term memory discriminatory perceptions have been recorded in monkey parietal cortex by neurophysiological techniques (Romo and Salinas 2001).

Whereas aspects of the evolution of frontal, parietal, temporal, and occipital lobes of the human brain can be documented by studying skulls, medial and deeply lying cerebral structures are inaccessible. They include the basal ganglia, limbic system, insular, anterior cingulate cortex, and in particular the hippocampus which is involved in making “permanent associative links between the pieces of information that define

a long-term memory...” (Miller and Cohen 2001), both explicit long-term memory and implicit long-term memory (Pennartz et al. 2011), as well as prospective memory (Gilbert 2011). This last-mentioned is demonstrated by neuroimaging studies that reveal hippocampal activity when activity in anterolateral prefrontal cortices is correlated with postponement of the execution of an intended action (Gilbert 2011).

The evolutionary appearance of prospective memory doubtless enabled *Homo erectus* children trying to copy a knapper of stone tools to interrupt their attempts in order to attend to a demonstration of how a skilful knapper performed precise and accurate manual operations. Interestingly, “the hippocampus and prefrontal cortex are coactive in early adolescence regardless of task demands or performance” to a far greater extent than later on in life (Finn et al. 2010). Given the likelihood that at twelve years old, a small-brained early *Homo erectus* was almost an adult, with communicative skills no greater than those of our four year-old children, the variety in Paleolithic techniques was slow to appear. Nevertheless, in Africa by 1.3 Ma, there are Paleolithic artifacts that imply human recognition of alternative volumetrical concepts of symmetry (see also, Wynn and Coolidge 2010) and performance of correspondingly separate bifacial knapping sequences for reducing stone, not only “Acheulian” but also (de la Torre et al. 2003) discoidal or “Levalloisian.” By 0.8 Ma, there is evidence of alternative (self-determining) behavioral chains of knapping behavior, excavated together, implying recognition of the irreversibility of the respective reduction sequences of stone by early humans (Walker 2009; Walker et al. 2013, 2016a). By at least 1 Ma, evidence of fire at Paleolithic sites in Africa, and by 0.8 Ma in Israel and Spain, implies cognitive ability to approach and tend fire, rather than to avoid hurtful flames and burning embers.

It is noteworthy that, unlike humans, great apes never put objects together to make a tool by assembling them, whether in the wild or in the laboratory. In stark contrast, on the other hand, they often take a composite object apart, so as to try to use a piece of it in order to gain access to something that they can see, though they never put separate pieces together in order to make a composite tool (Bräuer and Call 2015; Manrique and Call 2011; Pouydebat et al. 2005). Producing a functional tool by dismantling, breaking a branch into smaller pieces, or chewing or trimming off leaves does not necessarily require a complex hierarchical plan of action, nor even a mental representation of the intended end product. It may suffice to identify the affordances of the

new tools, “accidentally” produced, and compare them with the task requirements in order to see whether they make a good match. It is well-nigh impossible to manipulate different substrates randomly (branches, leaves, stones, and so on) and thereby put together a new and more efficient tool. To make a tool by assembling elements implies a mental representation of an intended “to-be-but-not-yet-existing-tool” composed from the disparate elements. Producing tools through random manipulation does not require a representation of a “tool-to-be,” merely appreciation of the new tool as being fit for purpose, after comparing new or current tools with the task requirements.

In experiments attempting to demonstrate fabrication by great apes of tools for future use (Bräuer and Call 2015), *both* the tool features *and* the task were available together for making comparisons. However, producing a new tool by putting pieces together requires *mental representation* of the “to-be-but-not-yet-existing-tool,” as well as comparison of it with the task requirements (random manipulation of substrates will never work). All the studies that have been reviewed here indicate that great apes are extremely inventive and have a good grasp of their physical world. They are skilled with tools and rapidly identify their functional properties in relation to the task in hand. They are capable of insightful problem-solving, but it is far from clear that they have the capacity for foresight that would allow them to represent flexibly not only things that are but also things that might be or will be. Very likely, great apes can neither assemble tools nor manage false-belief attribution because they suffer from one and the same cognitive limitation. Representing an imaginary world while faring in the real one is a very demanding ability that requires a capacity to blend reality among different potential spheres. This is what allows us to understand that another individual can have an image or understanding of the world that is different from our own, and, moreover, one that may turn out to be true or untrue.

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GLOSSARY

Acetylation chemical transference of an acetyl functional group from one molecule to another

Afferent (neuron) a neuron that transmits incoming sensory information to the brain

Affordance the possibility of an action on an object or environment

Alloparenting parental care provided by an individual toward a non-descendent young

Anterior/antero— at the front of, in front, frontal, forward

Anteroventral lying both forward and bellyward or below

Articulatory suppression the process of inhibiting memory performance by speaking while being presented with an item to remember; usually, it is intended to control for the possibility that using language (such as verbal labels) may help with the coding or recall of information

Artifact something made by somebody

Afferent/efferent afferent neurons bring sensory information to the central nervous system and brain/efferent nerves transmit impulses from the brain and central nervous system to muscles and organs

Amygdala an almond-shape group of neurons in the medial part of the temporal lobe of the brain, integrative center for emotions, emotional behavior, and motivation; it forms part of the limbic system of subcortical structures within the brain

Anthropoid Primates that include monkeys (which have tails) and apes (which lack tails), and of course humans

ASPM and MCPH1 gene complexes (abnormal spindle-like microcephaly associated protein and microcephalin-1 gene complexes)

Australopithecines extinct bipedal precursors of humans which lived in Africa between 4.5 and 1.5 Ma

Australopithecus garhi a species of australopithecine that lived about 2.5 Ma in East Africa

Autonoesis conscious awareness, characterized by conscious recollection of what we did or might have done in the past, and by imagination of future situations or happenings, thereby enabling us to examine our own thoughts

Axon elongated part of a neuron cell

Basal ganglia (or basal nuclei) nuclei in the temporal lobe of the brain, concerned with smooth performance of voluntary movements; they lie below the cingulate gyrus and include the corpus striatum (striped body) that has a dorsal part comprising the caudate nucleus (tail) and putamen (shell), and a ventral part comprising the nucleus accumbens (leaning nucleus) and olfactory tubercle, as well as the globus pallidus (pale globe), ventral pallidum, substantia nigra (black substance), subthalamic nucleus, and ventral tegmental nucleus; the basal ganglia lie on both sides of the thalamus and have wide-ranging neuronal connexions throughout the brain, and the ventral pallidum is regarded as a significant part of the limbic system (see limbic system)

Basolateral below and to the side of

Belief attribution the consideration that another individual divines correctly what you know to be correct. A belief can be true or false depending on whether it is congruent or incongruent with the state of affairs

Bonobo *Pan paniscus*, formerly called “the pygmy chimpanzee,” closely related to the chimpanzee (*pan troglodytes*). Both species diverged from each other around 2 million years ago

Broca’s area an area of the lower part of the left side of the frontal lobe of the human brain containing neurons associated with speech

Canonical canonical firing of neurons refers to their encoding of selected responses to inputs, such as watching the action of another individual; canonical encoding, or standardization of information to be transmitted, facilitates its subsequent transformation for an active response where appropriate

- Catarrhine** based on their facial characteristics catarrhine refers to anthropoid Primates of the Old World
- Caudate nucleus** see basal ganglia
- Causal understanding** understanding of causal relationships; usually applies to reasoning about causes and effects
- Central sulcus (a.k.a. Rolandic fissure)** separates the frontal and parietal lobes of the brain
- Centripetal flaking** striking toward the center of a prepared surface of a core
- Cerebellum** part of the brain, particularly involved with fine control of the muscular activity
- Cerebrum** cerebral, pertaining to the brain, particularly, those parts, anterior to, or above, the cerebellum
- Chaîne opératoire** a French term, sometimes called a “reduction sequence” in English, which refers to a sequence of stone-knapping
- Chopping-tool** a cobble or stone with a simply flaked edge, usually lacking any other signs of flaking
- Chromatin** a complex formed by deoxyribonucleic acid, DNA, and a histone protein
- Chunking** the breaking up of information into chunks which facilitates committing them to working memory or short-term memory; it consists generally in clustering together disparate pieces of information that share a common trait to reduce the information loads on working memory
- Cingulate cortex/cingulate gyrus** an internal (medial) part of the cerebral cortex
- Cleaver** an elongated stone with a single flaked transverse (“tranchet”) edge
- Combinativity** ability to arrange materials differently in alternative coherent ways
- Comparative psychology** the scientific study of the behavior of different animal species. It frequently seeks to compare the behavior of human and nonhuman animals to gain insight about the cognitive capacities of the species involved. The pioneering research of Wolfgang Köhler with chimpanzees illustrates the kind of work referred to when the term comparative psychology is used in this book
- Conchoidal flaking (stone)** striking a flake off a stone on which a concave shell-like (“conchoidal”) flake scar is left, whilst the struck flake bears a convex shell-like surface

Concrete operation (cognition Piaget) the capacity of young children to develop logical thinking about concrete or specific matters whilst not yet able to deal easily with abstract matters (the third of Jean Piaget's stages of psychological development in children)

Cortex the highly convoluted outer layer of the brain

CREB-1, CREB-2 cAMP-response-element binding proteins 1 and 2, respectively

Cuneus a posterior part of the parietal lobe of the brain

Cytoarchitecture refers to a group of cells which show a structural arrangement

Débitage a French word referring to any products knapped from a core, such as flakes, blades, flake-blades, slivers, spalls, and fragments

Declarative memory/explicit memory capacity to speak about matters that have been remembered. An example of declarative memory is if you can give verbal answer to the question: What have you learnt?

Dendritic spines microscopical structures present on the external surface of neuron cells

Dentate gyrus a part of the hippocampus in the temporal lobe of the brain

Developmental psychology psychological study of the development through the whole life span, focusing on ontogeny

Dorsal/dorso— relating to the back of a creature

Early Pleistocene (a.k.a. Lower Pleistocene) the time period between 2.58 and 0.78 Ma

Efferent see motor neuron

Eidetic image image retained briefly in the brain after something that had been seen is no longer visible

Encephalization evolutionary tendency toward increase over time in brain mass relative to body mass

Engram (neuropsychology) sometimes called a latent memory trace, an engram is not yet a memory while providing biophysical conditions for giving rise to memory in neurons (The word is used in Scientology to convey the notion of a mental image stored in the mind but this notion is not supported by neurophysiological research.)

Epigenetic biological inheritance owing to cellular processes other than those of nuclear deoxyribonucleic acid, DNA

Episodic memory the memory of episodes, scenes, activities, behaviors, conversations, dreams, connecting with an individual's personal past, and accompanied by a specific type of conscious awareness; the ability to talk about such memories leads them to be called explicit or declarative memories

Episodic-like memory usually is employed to infer that nonhuman animals have knowledge about where to find something, being a recollection of the kind "what/where/when" that was proposed by Endel Tulving, who argued that it is accompanied by a specific kind of awareness that he termed autonoetic consciousness; because episodic memory depends on declarative recall it is limited to humans and almost impossible to demonstrate in nonverbal beings whose memory responses can seem to be episodic-like

Entorhinal cortex part of the temporal lobe of the brain close to the hippocampus

Evolutionary anthropology the study of human evolution with particular reference to inferences drawn from Charles Darwin's theory of natural selection in the origin of species and their subsequent evolution

Explicit memory see episodic memory

Extinction (of a behavior) refers in the context of operant conditioning (instrumental conditioning) to disappearance of a pre-potent response or behavior when no longer followed by a reward

Extrastriatal inner part of the brain between the corpus striatum of the basal ganglia and the cerebral cortex

extrastriatal motion-sensitive (V5/MT) area of the middle temporal lobe of the brain

Façonnage a French word meaning fashioning, referring to the shaping of stone artifacts, such as hand-axes and cleavers

False belief a false-belief understanding is the understanding that someone's belief or representation about the world may contrast with reality or diverge from it

Forethought capacity to think ahead

Foresight/foresee capacity to envisage outcomes

Formal operation (cognition) the capacity, beginning in early adolescence, to think in abstract fashion without depending on concrete manipulation (the fourth of Jean Piaget's stages of psychological development during human growth)

Fornix a medially situated group of neurons the fibers of which form a fork between the hippocampus and other neuronal structures further forwards that include the amygdala

Forward thinking capacity to plan for future outcomes

Frontal lobe/frontal gyri the most anterior parts of the brain

Functional magnetic resonance imaging a neuroimaging technique (commonly called CAT scanning or computer-assisted tomography)

Glacial period an ice-age

Globus pallidus see basal ganglia

Goal attribution attributing a goal to the behavior of a subject

Gorilla a panin great ape, *Gorilla gorilla*

Great ape a hominoid belonging to panins or pongins

Gyrus gyri, a fold or convolution of the external cerebral cortex

Habenula nucleus of neurons beside the thalamus associated with the basal ganglia and limbic system

Hand-axe elongated bifacially flaked stone artifact

Haptic relating to touch and tactile responses

Hierarchical knapping preparation by flaking a stone core such that one or more flakes (often of regular forms or shapes) can be struck from one surface of it

Histone proteins form complexes with DNA in chromatins

Hominin belonging to the tribe Hominini (australopithecines and *Homo*)

Hominoid belonging to the family Hominoidea (hylobatids, pongids, panins, hominins)

Homo genus of humans, past and present

Homo erectus a fossil (extinct) human species from between about 2 and 0.5 Ma

Homo ergaster an alternative name sometimes given to African *Homo erectus* from between 2 and 1.5 Ma

Homo heidelbergensis a fossil (extinct) human species in Europe between about 1 and 0.5 Ma, widely regarded as ancestral to *Homo neanderthalensis*, though various authorities recognize it in Africa during the same period

Homo neanderthalensis a fossil (extinct) human species from Europe to Central Asia between about 0.5 to 0.04 Ma (a.k.a. “Neandertal Man”)

Homo sapiens modern human beings (from about 0.3 Ma to the present day)

Homotaxial homotaxis, a notion of which an example might be the different geological times at which herbivory, frugivory, insectivory, omnivory, and carnivory arose in Australian marsupial mammals on the one hand, and elsewhere in placental eutherian mammals on the other; it was applied by Cambridge University archaeologist Grahame Clark to Paleolithic evolutionary trajectories in different parts of the world during the Pleistocene in order to interpret perceived chronological disparities

Implicit memory memory that usually does not inspire conscious awareness: for example, when watching the traffic when pedalling a bicycle we do not forget how to pedal usually, much less are we consciously remembering about how to do it

Impulse (behavioral) a behavioral response that escapes an individual's control

Impulse (of a nerve) transmission of a signal by a neuron

Inferior/infero— below, underneath

Inferior parietal lobule part of the parietal lobe of the brain

Inhibitory capability capability of an individual to inhibit, interrupt, restrain, or suppress an otherwise characteristic behavioral response

Instrumental conditioning see operant conditioning

Interglacial refers to period or conditions between two glacial periods (ice-ages)

Interoceptive refers to sensory impulses transmitted by nerves from bodily organs to the brain

Interoceptive Von Economo spindle cells large neurons especially found in the human insula, regarded as associated with rapid transfer of information in the brain

Intraparietal sulcus a groove within the parietal lobe of the brain

Insight accurate and deep understanding about something or someone

Insula the name of a medial part of the cerebral cortex

Kinase generic term for enzyme that catalyzes chemical transfer of a phosphate functional group from adenosine triphosphate to another molecule

kinesthesia refers to sensory impulses transmitted by nerves from joints and muscles to the brain.

Knapping (stone) the working or modification by hand of a stone by removal of flakes, slivers, spalls, and fragments

Knowledge attribution in psychology it refers to the notion that individuals make sense of their surroundings based on what they regard

to be the cause(s) and effect(s) of a phenomenon; it also can refer to recognition by an individual that another individual share the same knowledge about specific aspects of reality

Late Pliocene (a.k.a. Upper Pliocene) the geological period between about 4 and 2.58 Ma

Late Pleistocene (a.k.a. Upper Pleistocene) the period between the beginning of the last interglacial period about 128,000 years ago (0.128 Ma) and the end of the last ice age about 12,000 years ago (0.012 Ma)

Lateral refers to the side of something

Lexigram a token that stands in for a word, phrase, object, or concept.

Limbic system medial and deeply situated parts of the brain (including amygdala, basal ganglia, cingulate cortex, hippocampus, hypothalamus, and other groups of neurons) that are involved with relating the input from sensory nerves to the modulation by the brain of responses.

Lobe lobule, some large parts of the cortex of the brain are called lobes, and some smaller ones are called lobules

Logico-mathematical (cognitive) the term as developed by Jean Piaget refers to recognition of logical correspondences or relationships between things or concepts

Long noncoding RNA (lncRNA) ribonucleic acid not directly involved with coding

Long-term memory memory retained or stored of previous behaviors or matters (including fantasies and dreams); whereas when considered by clinical psychologists in terms of loss of memory, long-term memory often refers to periods of time measured in years, months, weeks, or days, by contrast experimental neurophysiologists may regard long-term restriction of neuronal memory as occurring in a matter of hours or less following an intracellular stimulus

Lower level explanation in comparative psychology it refers to systematic operations requiring little refinement or capacity for abstract reflexion in order to achieve specific goals

Macaque a kind of monkey belonging to the genus *Macaca*

Medial/medio— toward or at the midline (taken as running from the front to the back of the brain)

Mentalistic interpretation an interpretation of behavior that when applied to animals presumes that which it ought to have been the task of science first to have demonstrated, namely, that the mental basis for

their behavior often can be regarded as reflecting human mental processes and interpreted by analogy with these; in comparative psychology it is used often in opposition to the external reading of behavior in which a nonhuman animal predicts what another individual may do based on the regularities observed in the latter's past behavior rather than on the attribution to that individual of intentions, desires, or goals

Middle Pleistocene the time period between 0.78 and 0.128 Ma

Motor (neuron) a neuron transmitting “efferent” (outgoing) nerve impulses from the brain to muscles

Multimodal refers to groups of neurons in the brain that subserve sensory inputs without differentiating between them (sight, sound, touch, smell, sensations from joints and bodily organs, and so on)

Neandertal see *Homo neanderthalensis*

Neocortex neocortical (a.k.a. neopallium), the part of mammalian brains involved with perceiving sensation and causing motor responses

Neurogenesis production of new neurons, especially, in the brain of fetuses and infants, though it can take place throughout life

Neuroimaging a range of technical procedures for studying activity in the brains of living individuals (see Chap. 3 for references to different procedures)

Neuron a cell that is involved in transmitting information in the nervous system of an animal

Neurophysiology the physiological study of neurons and the nervous system

Noncoding RNA epigenetic regulators of gene expression impingement on gene expression by constituents of ribonucleic acid (RNA) that are not involved directly in the coding of inherited genetic material

Nondeclarative memory memory that usually is unspoken (or not otherwise declared explicitly by writing, sign-language, and so on), such as in habitual or routine behavior or activities, including learnt behavior such as dance routines; because it is not declared explicitly it requires the performance of an action in order to be detected

Nucleosome in the nucleus of a cell a nucleosome forms part of a chromosome and consists of deoxyribonucleic acid (DNA) associated with histone proteins

Olduvai Oldowan, relating to the Olduvai Gorge in Tanzania, and to the kinds of Oldowan stone artifacts typical of that site

Operant conditioning (a.k.a. instrumental conditioning) is based on the argument of B.F. Skinner that learning is a function of change in overt behavior and that changes in behavior are the result of an individual's response to events (stimuli) in its surroundings. Unlike classical conditioning (a.k.a. pavlovian conditioning) in which associations between unconditioned and neutral stimuli are formed that escape individual's control, here the individual's behavior is instrumental in that it can alter the environment and produce positive or negative consequences

Operculum (anatomy of the brain) is a Latin word meaning a small "lid" that is used to refer to parts of the frontal, temporal, or parietal lobes, which lie external to, or cover, the insula (see insula), and it can also refer to a part of the occipital lobe

Optogenetics neuroscientific procedures by which genes for light-sensitive proteins are introduced into cerebral neurons in order to monitor and control their activity precisely using light signals, and thereby throw light on how neurons react and interact

Orangutan a great ape belonging to the genus *Pongo*

Orthogonal flaking removal of flakes more or less in parallel to each other by alternate knapping a surface of prepared stone core often in opposite directions

Paleoanthropology the study of ancient human remains and behavior

Paleolithic refers to stone tools of kinds that were widely used by hunters and gatherers, and are usually earlier in time than "Neolithic" stone tools that are associated with the initial prehistoric cultivation of plants and domestication of animals. The word Paleolithic is made up from Greek words for "old" and "stone", in contrast to Neolithic or "new stone." In some parts of the Old World the two concepts are separated by a notional Mesolithic ("meso" means middle or intermediate) in consideration of a tendency for the knapping of particularly small stone points to be seen in assemblages left by hunters and gatherers at the close of the last Ice Age and shortly after it. In regions around the Mediterranean Sea and in southwestern Asia and Europe, there is the widespread usage of the terms Early or Lower Paleolithic, Middle Paleolithic, and Late or Upper Paleolithic, on the grounds that significant differences can be discerned in the main types of stone artifacts found in assemblages from successive periods of Pleistocene time. In most of Africa, the terms Old Stone Age and Middle Stone Age are preferred by many Paleolithic archaeologists for reasons that are beyond the explanatory scope of this book which uses Paleolithic for both

- Paleoneurology** the study of fossil brains, particularly by reconstructing their anatomy by reference to the structure of fossil skulls
- Pallidum** a part of the brain, see basal ganglia
- Pan*** the genus of great apes that consists of the chimpanzee, *Pan troglodytes*, and the bonobo, *Pan paniscus*
- Panin** refers to the tribe Panini that comprises great apes belonging to the genera *Gorilla* and *Pan*
- Parahippocampal gyrus** part of the temporal lobe in close association with the hippocampus
- Parieto-occipital** rear parts of the cerebral cortex separated by a sulcus or groove
- Pebble-tools** cobbles or stones from which a few flakes had been removed by knapping that left a sharp edge on the artefact
- Perspective-taking** the suspension of an individual's point-of-view in an attempt to view a situation as another might view it
- Phosphorylation** chemical transference of a phosphate functional group from one molecule to another
- Planning** the process of thinking about and organizing the activities required to achieve a desired goal; it involves the creation and maintenance of a plan, such as psychological aspects that require conceptual skills
- Platyrrhine** based on their facial characteristics platyrrhine refers to anthropoid Primates of the New World
- Pleistocene** period between 2.58 and 0.012 Ma
- Pliocene** period between about 5 Ma and 2.58 Ma
- Plio-Pleistocene** usually refers to an imprecise period between about 4 and about 1.5 Ma
- Polymodal** refers to groups of neurons in the brain that subserve sensory inputs without differentiating between them (sight, sound, touch, smell, sensations from joints and bodily organs, and so on)
- Positron-emission tomography** a technical procedure for studying activity in the brains of living individuals
- Precentral (brain)** a posterior part of the frontal lobe lying anterior to the central sulcus; it is concerned with motor control of muscles
- Precuneus** a part of the cerebral cortex lying posteriorly in the parietal lobe of the brain
- Premotor** the premotor cortex of the frontal lobe of the brain lies anteriorly to the precentral cortex; it is concerned with motor control of muscles

Preoperational cognition (Piaget) the cognitive stage of infants prior to their development of logical thinking about concrete or specific matters

Pre-potent in the context of this book the term is used to refer to overwhelming tendencies of an animal to carry out a particular behavior regardless of alternative possible behaviors that otherwise might advance achievement of a desirable goal; pre-potent responses have a natural significance in connection with survival (such as food or sex) though a neutral behavior can become prepotent when followed, repeatedly and systematically, by presentation of a reward such as food

Primates the biological order of Mammals which includes prosimians, monkeys, great apes, and humans

Procedural memory the nondeclarative memory of long-term remembered habitual behavior, nevertheless open to conscious modification, such as pedalling a bicycle, sawing a log, taking part in a square dance, and so on

Prospective memory future thinking; the capacity to envisage future outcomes or behaviors

Psychophysical refers to an experimental methodology that relates varying neuronal responses in the brain to varying stimuli, under controlled laboratory conditions

Putamen a neuronal structure in the brain (see basal ganglia)

Reinforcement refers in operant/instrumental conditioning to the process by which a response that is followed shortly by the presentation of a reward or circumstance agreeable to the subject is more likely to be repeated in the future

Retouch secondary knapping of the edge of a stone artifact

Reward offered to subjects in operant/instrumental learning to favor achievement of a goal. It may be an object (such as food or money) or an action (such as sex or play) which is presented immediately after the subject has performed the desired behavior or response

Rhesus monkey a monkey of the species *Macaca mulatta*

RNA-editing a technique by which a polymerase enzyme can modify specific nucleotide sequences in a molecule of ribonucleic acid

Rule-guided interpretation an interpretation of a rule in a new factual situation, which is grounded in previous experience

Rostral/rostrum behind, posterior

Secondary knapping see retouch

Semantic memory declarative memory involving conscious recollection of matters that can be named separately

Short-term memory memory retained or stored during only a short period of time of previous behaviors or matters (including fantasies and dreams)

Whereas when considered by clinical psychologists in terms of loss of memory, short-term memory often refers to periods of time measured in years, months, weeks, days, or even hours (for instance, Alzheimer patients who ask for breakfast having forgotten they had breakfasted an hour before), by contrast experimental neurophysiologists may find short-term restriction of neuronal memory within a few minutes after an intracellular stimulus, which implies that such very short-term working attention is somewhat different from the concept of short-term working memory employed by psychologists (see working attention, working memory)

Somatic referring to the body

Somatosensory refers to sensory inputs to the brain from parts of the body

Stimulus/stimuli (brain) an event or intervention evoking a specific neuronal response. In classical (Pavlovian) and operant (Skinnerian) conditioning, it is regarded often as the trigger of a specific response

Striatum/striate see basal ganglia

Superior frontal gyrus a convoluted area of the frontal lobe of the brain

Supplementary motor tegmental area a part of the brain stem, lying below the cerebral cortex

Synaesthesia a perceptual phenomenon in which stimulation of one sensory or cognitive pathway leads to automatic, involuntary experiences in a second sensory or cognitive pathway; for instance when the color red is perceived as a high-pitched sound

Short RNA elements (siRNA, piRNA, microRNA) short ribonucleic acid elements, some of which are involved in epigenetic inheritance

Substantia nigra see basal ganglia

Sulcus groove or cleft

Synapse refers to a microscopical separation between neurons across which transfer of information between them may take place

Thalamus/thalamic nuclei see basal ganglia

Temporal (lobe) a lobe of the brain

Theory of mind (ToM) the ability of an individual to attribute mental states (beliefs, intents, desires, pretending, knowledge, and so on) to itself and others and to understand that others have beliefs, desires, intentions, and perspectives that are different from those of the individual

Tool-kit (Paleolithic archeology) an assemblage of artifacts

Tool-making the artificial preparation of an artifact for use as a tool

Tool-use the use as a tool of an artificially prepared artifact

Transcranial magnetic stimulation (TMS) a neuroimaging technique

Transcription factors proteins involved in converting or transcribing deoxyribonucleic acid into ribonucleic acid

Transcriptome the full range of messenger ribonucleic acid expressed by an organism

Sensory (neuron) see afferent neuron

Ubiquitination addition of ubiquitin to a substrate protein, which can mark proteins for degradation via the proteasome, alter their cellular location, affect their activity, and promote or prevent protein interactions

Ventral/ventro— bellyward

Visual cortex the cerebral cortex concerned with sight in the occipital lobe

Visuospatial concerned with sight and space

V5/MT a neuronal area in the middle of the temporal lobe of the brain which is concerned with the forward transmission of visual information (the fifth forward of a series of neuroanatomical relay stations for forward transmission of information from the occipital visual cortex)

Wernicke's area an area in the temporal lobe of the brain involved with processing acoustic information

What/Where/When memory a concept of episodic memory put forward by Endel Tulving

White matter (brain) neurons with myelin sheaths around their axons

Working attention an aspect of short-term working memory which applies to brief retention of information that may or may not be processed further

Working memory a limited memory capability for temporary retention of information for further processing

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